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ON THE DEVELOPMENT AND LIFE HISTORIES OF THE TELEOSTEAN FOOD- AND OTHER FISHES.

[PLATES I. TO XXVIII.]

BY

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XIX.—*On the Development and Life-Histories of the Teleostean Food- and other Fishes.*

By Professor W. C. M'Intosh, F.R.S., and E. E. Prince, B.A., St Andrews Marine Laboratory.* (Plates I. to XXVIII.)

(Read 18th June 1888.)

For Table of Contents see end of paper.

I. General Remarks.

Until very recently existing information concerning the eggs and oviposition of British fishes, and more especially marine fishes, was of the most fragmentary character. In the standard works upon Ichthyology, such as Owen's *Anatomy of Vertebrates* (vol. i. Fishes), it is comprised in a few vague sentences; while the original papers published by British ichthyologists are not numerous, and refer, for the most part, to fresh-water species. Within the last few years, however, attention has been more systematically directed to the subject, and the enlightened views of the late Royal Commission on Trawling, and more especially of its chairman, the late Earl of Dalhousie, has given a fresh impetus to the study of the development and life-history of our food-fishes, as preliminary to a thorough investigation of their habits, food, so-called migrations, and general life-history.

The following paper comprises the first results of our recent work at the St Andrews Marine Laboratory.

Though much has been done by foreign observers of late years in regard to the development of marine fishes, yet the cod and herring only, amongst those conspicuous by their economic value in this country, have been specially dealt with.

It was therefore necessary, even at the risk of repeating some observations already known to science, to examine as thoroughly as possible the ovarian growth, oviposition, hatching, and development of such of the important white fishes as could be obtained, and to fill up the gaps in our knowledge of the period between the escape of the embryo from the egg, and the young, though advanced, forms known to naturalists and fishermen.

* The authors have to acknowledge the courtesy of the Fishery Board for Scotland, under whose auspices the work has been accomplished, and to whom all credit is given. Grants from the Royal Society (Government Grant) and from the British Association have also been of great service in regard to assistance and apparatus. To Dr Scharff, B.Sc., now of the Museum of the Royal College of Science, Dublin, for valued aid of various kinds in 1886, and to Dr J. Wilson of St Andrews, for help in making sections, our acknowledgments are also due. When cruising in the Fishery Board tender "Garland," Mr W. L. Calderwood, B.Sc., and Mr H. E. Durham, B.A., also kindly gave assistance. It may further be stated that the first part of the paper, containing the development of the food-fishes and their early larval condition, was mainly the work of Mr Prince; while the account of the post-larval stages, the development of *Anarrhichas* and the salmon, was the work of Dr M'Intosh. Mr Prince added further notes on the structure of the later stages of other forms.

The ova of about forty British fishes have been examined, and in most cases the development of the young before and after leaving the egg, as far as possible, followed. The period over which the special observations extended commenced with the work for H.M. Trawling Commission in 1884, when the talented chairman (Lord Dalhousie) placed every encouragement (personal and administrative), and all the facilities in his power for pursuing the subject as thoroughly as time would permit. The experience of former years at St Andrews and elsewhere has been made available, especially in regard to the growth of marine fishes, and to the structural features in the later stages of the salmon.

The ova examined at St Andrews may be conveniently arranged in two divisions, viz., Pelagic or floating eggs, and Non-Pelagic or demersal eggs.

Under the former head twenty-three species may be grouped, viz., Long-Rough Dab, Turbot, Plaice, Lemon-Dab, Craig-Fluke, Common Dab, Common Flounder, Sole, Müller's Topknot, Ling, Five-bearded Rockling, Cod, Haddock, Bib, Whiting, Poor Cod, Green Cod, Pollack, Frog-fish, Skulpin, Lesser Weever, Sprat, and Grey Gurnard. Besides the foregoing, the Common Eel and the Conger have been examined; but their pelagic or demersal character has not been finally determined.

The non-pelagic ova include at least fourteen species, besides a few doubtful forms of which the ovarian eggs alone have been under consideration. This (demersal) group embraces the Herring, Smelt, Salmon, Trout, Bimaculated Sucker, Wolf-fish, Shanny, Viviparous Blenny, Montagu's Sucker, Lump-sucker, Goby, Armed Bullhead, Cottus, Fifteen-spined and Three-spined Stickleback, Sea Bream, Gunnel, &c., besides the Cyclostome—*Myxine*. Amongst the doubtful eggs are those of Yarrell's Blenny and the Sand-Eel (*Ammodytes tobianus*).

II. The Mature Ovum.

General Features.—The mature ovum of osseous fishes is generally of comparatively small size, spherical in form, and more or less translucent. Two parts may be distinguished, viz., a protective external capsule (Pl. I. figs. 1–4, *zr*), and a contained vitelline mass (*y*), the latter consisting of a globe of food-yolk, with interfused germinal matter. Upon being placed in water, the ova of some species float near the surface and throughout the water; these, as already pointed out, form the pelagic group; while in other species the eggs sink to the bottom, and form the second group, viz., the demersal or non-floating eggs. The first group exhibit in a striking way the feature characteristic of pelagic structures, viz., a colourless translucency; while the second or demersal group are less delicate in appearance, and often tinted in a marked manner. Thus the freshly extruded ova of *Cyclopterus lumpus* are of a brilliant purplish rose, or a subdued green or yellow tint, which soon, however, fades away, and the eggs become more translucent. The ova of the salmon, by their rich orange colour, afford a familiar example of tinted demersal eggs; while those of many species of Stickleback (*e.g.*, *Gastrosteus spinachia*) are of a transparent amber-tint. Such coloration, as just noted, like the whitish opacity of the ovarian

ovum, may be transient and give place after extrusion to an imperfect transparency. The ova of *Ammodytes tobianus* present a marked example of this, for while contained in the ovary they are of a bright orange colour—the ovaries on this account forming a bilobed orange-tinted mass in the abdomen of the nearly ripe female, but the eggs when ready for extrusion, and indeed while passing to the oviducal aperture, would appear to become colourless. Pelagic eggs usually float loosely together or singly, and do not adhere to each other, save in certain noticeable instances, of which *Lophius piscatorius* is an interesting example. Agassiz first described the floating eggs of this familiar fish as adhering together in long bands near the surface (No. 1, p. 280), but even in this case eggs may become detached and float free (No. 2, p. 16). Professor E. van Beneden describes some minute isolated and agglutinated eggs which he was not able to determine, but believed that they belonged to a species of *Lota*, and he supposed that, after being deposited in a mass, they "remain for some time adherent one to another, and afterwards separate, and then float free from all adhesion, on the surface of the sea" (No. 25, p. 41). This surmise is perhaps questionable, and Van Beneden, indeed, himself adds—"I never saw the eggs become detached from one another" (p. 42); and they probably, therefore, belonged to two different species. Eggs similar to those of E. van Beneden were obtained by Haeckel on the coast of Corsica. They formed agglutinated masses of various volume and form—the ova being in fact imbedded in a gelatinous substance.* Pelagic ova, if ever adherent, possibly may soon become detached, but eggs deposited on the sea-bottom, in masses, adhere together most strongly, though in an advanced stage they are less firmly united, this loss of adherent property in such a form as *Cyclopterus lumpus* taking place only after the lapse of a considerable interval, often many weeks, when the capsule becomes softened, and changes occur in its physical character, probably to facilitate the liberation of the contained embryo. Usually, however, these eggs cling together if undisturbed (even when dead) for long periods. The adhesive character which Von Baer was the first to notice in certain Cyprinoids† is due to a mucilaginous ovarian secretion bathing the eggs, and acting as a lubricant during extrusion. On exposure to water, it has the property of hardening, as in many similar instances both in vertebrates and invertebrates; and, in the case of adherent eggs, it acts as a cement, binding them together so firmly that they can be separated only with difficulty; and the points where the adjacent eggs were in contact show prominent scars or facets after separation (Pl. I. figs. 2, 3, and 4, *x*).

A marked translucency of both capsule and egg-contents usually indicates the healthy

* Mr Rattray has recently submitted to us examples of pelagic ova from the west coast of Africa, which are also bound in masses by a connecting substance converted by reagents and alcohol into a thread-like meshwork. Threads of a like character were noticed in some ova sent by M. Millet many years ago to the French Academy of Sciences. They were evidently demersal eggs, for they were attached to a wooden barrel hoop by the elastic threads, the latter forming a felted meshwork, which Millet supposed to be produced by the parent-fish (No. 110, p. 342). They were procured in 14° 15′ N. lat. and 20° 30′ W. long. The eggs Mr Rattray kindly sent to St Andrews were obtained (in the s.s. "Buccaneer" Expedition) in lat. 1° 17′ 6″ N., long. 13° 54′ 4″ W. *Vide* Remarks on these by Mr J. T. Cunningham, *Trans. Roy. Soc. Edin.*, xxxiii. i. p. 108, pl. vii. fig. 7.

† *Untersuchungen über die Entwickelungsgeschichte der Fische*, Leipzig, 1835, p. 7.

living egg, especially in the case of pelagic ova, and also to a certain extent in demersal forms. This translucency is due to the disappearance of the granules in the yolk of the ovarian egg when ripe. Sometimes, however, eggs which are not perfectly mature, *i.e.*, lack the translucency of the ripe ovum, may yet be fertilised, and their embryos in due time liberated. This was frequently the case with imperfectly ripe eggs of *T. gurnardus*, which, though presenting slight opacity, were successfully hatched. Occasionally eggs of the species just named exhibit a remarkable pinkish or reddish coloration, the oil-globule being of a dark tint (Pl. XVI. fig. 10). The cause or meaning of this abnormal appearance is undecided; the eggs, of course, were not fertilised, and did not develop; indeed, this coloration has only been seen in dead eggs. Pelagic eggs, when dead or unhealthy, show a great increase in the perivitelline space, and sink to the bottom of the tanks. Sometimes living eggs, from various causes, such as a change in the specific gravity of the water, sink, this being frequently the case with *T. gurnardus;* yet when the water is violently stirred, or when removed from still water for examination, and then emptied into the tanks, they again often assume their buoyancy. This may be due to the disengagement of particles of foreign matter, such as sand, though this is not always evident. The eggs of *Molva vulgaris* (Pl. I. fig. 10) are less buoyant than some other Gadoids, *e.g.*, *Gadus morrhua* and *G. aglefinus*, and sometimes, though living, sink to the bottom in quiescent water, yet successfully develop. The ova of the ling are indeed more delicate, and more susceptible to unfavourable conditions than those of the cod and haddock. The addition of spirit to a vessel containing them causes them to rush to the side of the vessel, and cling to it with tenacity. The hardy character of certain pelagic eggs and their vitality was shown in many cases at the Laboratory. No difficulty was found in developing eggs fertilised at sea and conveyed long distances, in some cases after travelling in earthenware jars for three or four days. Eggs of the cod contained in such jars, three-fourths filled with sea-water, reached the Laboratory on the fourth day after fertilisation, and though most of the eggs had sunk to the bottom, and the water was offensive with putrid matter—Infusoria, Bacteria, and Spirilla being abundant, yet many of the eggs still floated at the surface, and the hearts of the embryos pulsated regularly. The effect of cold is to retard development, but is not detrimental unless extreme. In one instance a series of the eggs of the haddock were floating buoyantly in the tanks at 6 P.M., but next morning the glass vessel was covered with a coating of ice, on breaking which most of the eggs fell to the bottom, and in these the yolk and germinal area were found to be much shrunken and corrugated, leaving a wide space round the vitelline mass. A few only survived, these having apparently remained under the trickle of the supply pipe.* That pelagic eggs float in sea water, while they sink in fresh water, or in sea water having an admixture of fresh, Professor BAIRD has shown to be due to the fact that their specific gravity is about 1·020 or 1·025.†

* *Vide Nature*, June 1886.

† Of this floating property, the oldest fishermen, BAIRD adds, had not the slightest idea; they thought "that the females deposited their eggs on the rocks, where they were visited and impregnated by the males. . . . . They had

Pelagic Ova.

General Remarks.—The pelagic nature of the ova of so large a number of valuable food-fishes removes them altogether from many of the vicissitudes which befall demersal eggs. Their transparent glassy nature, minute size, and enormous abundance, sufficiently provide for their safety and the increase of the species. Pelagic ova are by no means common in the stomachs of fishes, while ova deposited on the bottom (*e.g.*, those of *Cyclopterus*, *Cottus*, and *Clupea harengus*) are eaten by many fishes with great avidity, yet the numbers of one of these at least are, so far as can be made out, by no means seriously affected. How much more surely, then, is the multiplication of those with pelagic ova provided for? As a rule, they are deep enough to escape the vicissitudes of the immediate surface, and in our country are seldom stranded on the beach in numbers sufficient to attract attention.* The larvæ which escape from them are also minute and translucent, and thus are less prone to attract the notice of predatory marine forms; moreover, they soon become very active, while their purely pelagic life gives them a vast area for their safe development.

The contrast between such types and the condition, for instance, in *Cottus*, is marked. In the latter the ova are deposited between tide-marks in masses, and are often devoured by other fishes, and it may be by predatory birds and mollusks. The comparatively large young are conspicuous objects, and can only escape by keeping within reach of tangles and other sea-weeds, a constant reduction of their numbers taking place, notwithstanding their defensive armature, during the somewhat slow growth to the adult condition. It is possible, indeed, that though the egg-capsules in *Cottus* are much denser, and the embryos larger and more highly developed than in the cod, a much greater number of the latter proportionally reach maturity than in the case of the former.

On the eastern shores pelagic ova begin to appear at the end of February, though there is no reason why some should not be found earlier, as Dr J. Murray tells us they are on the west coast (Clyde district), and a kind of succession of those of different species occurs throughout the spring, summer, and autumn. Amongst the earliest are the ova of the plaice, *Motella*, and the large egg with the spacious perivitelline space, the larval form issuing from which is described subsequently. Those of the Gadoids, such as the cod, haddock, and whiting, next appear, and also those of the flounder and dab, while towards the end of the month the eggs of the gurnard are also captured. April is characterised by the abundance of pelagic ova, the maximum perhaps being attained towards the latter part of the month, when the ova of the sprat† and other forms swell the list. As an

at times noticed the little transparent globular bodies in the water; but it never occurred to them that they were the eggs of any fish. They may be found at the surface in common with the eggs of pollack, haddock, and probably other species of the cod family, when the sea is smooth, but when the water becomes rough they are carried to a depth of several fathoms by the current, though the tendency is to remain near the surface" (No. 8, p. 715).

* G. O. Sars found, however, that they were so at Lofoten.

† Hensen first noticed the pelagic ova of the sprat, and his observation has been corroborated by J. T. Cunningham and ourselves. Other Clupeoids, as shown by Raffaele, also have pelagic eggs.

example of the duration of a particular kind of ova in the bay, those of the gurnard may be taken; for, appearing in April, they continue throughout May, June, and even part of July, being very abundant in June. It is clear, therefore, that with rapid growth, the differences in size between the post-larval forms produced from the ova at the extremities of the period must be considerable.

Distribution.—Nothing was more striking, in the investigations in connection with H.M. Trawling Commission in 1884, than the abundance of the pelagic ova in the upper regions of the water, and indeed throughout it. They are not usually found quite at the surface, but as soon as the tow-net is sunk a fathom or two, they occur almost in every haul on suitable ground. Though on the banks frequented by the cod, haddock, and whiting, these pelagic ova are in greatest profusion at the breeding season, yet they are met with during many months from January till late in autumn, a continuous discharge of ova taking place from one or other group having this habit. Moreover, it is clear that the provision by which only a portion of the ovary in most fishes with pelagic eggs becomes ripe at a given time, greatly prolongs the spawning period, and tends to intensify the feature just mentioned. It is possible indeed to form an estimate of the number of spawning fishes in a given district by the abundance of pelagic ova, or the contrary. It is only necessary to illustrate this by reference to the surface of Smith Bank, off the coast of Caithness, where the ova and embryos were in vast numbers in the beginning of April, so much so that the area resembled a vast hatching-pond, even the sea-birds feeding in long lines on such as the currents swept to the surface. The same feature was shortly afterwards noticed, along with Lord Dalhousie, off the Island of May, though both eggs and embryos were less numerous than in the former case.

Again, recent investigations with the trawl-like tow-net on the bottom show that a vast number of pelagic ova, such as those of the cod, whiting, rockling, sole, flounder, gurnard, sprat, and other forms, are to be found there—when the large mid-water net and the surface-net are nearly devoid of them. Whether this aggregation of ova is due to cold at the surface or to the effect of currents has not yet been determined, but it is a feature of great interest.

*Sizes of Ova.**—As an example of the variety of pelagic ova common to the sea beyond the Firth of Forth in April, the following measurements from spirit-preparations are interesting. The ova were collected by the tow-net (sunk a fathom or thereabout) in the usual manner, and then placed in strong spirit, which caused considerable contraction, probably from ·1 to ·15. A very few measured ·0216 of an inch, others had a diameter of ·023, ·03, ·033 (probably *Motella*), ·035, ·0366, ·04, ·043, ·045, ·046, ·05, the largest number ranging over the area covered by the last five, which probably included cod, haddock, ling, &c., ·056, and a very few at ·058 and ·083 of an inch. A little variation appears to occur in each species. The average in fresh specimens of the haddock is ·056, the blastodisc being ·033; plaice, ·0716; ling, ·0916, and the oil-globule, ·031;

* A table of sizes of ova from Raffaele is given by one of us, in a Report on the Pelagic Fauna of St Andrews Bay, *Seventh Annual Report, Fishery Board for Scotland*, 1889.

cod, ·06; grey gurnard, ·055, and oil-globule, ·0116; lemon dab, ·053; flounder, ·038; common dab, ·033; skulpin, ·025 to ·030; sprat, ·044 in long diameter, ·039 in short diameter; sole, ·045.

The Egg-Capsule, with Remarks on the Reproductive Organs and Period of Spawning.

Few points in the constitution of the ovum afford more matter for controversy than the origin and significance of the external protective membrane.

The twofold division of egg-membranes, due to Prof. E. van Beneden (No. 24, pp. 228–30), and founded upon their derivation, is both natural and convenient, viz., (1) membranes differentiated from the cortex of the egg-mass itself; (2) membranes formed *ab extra* by the cells of the ovarian follicle. It is generally agreed that the egg-capsule of Teleostean ova belongs to the first division. Cunningham, however, does not adopt this view, and the "vitelline membrane" of his earlier papers he now considers to be an extra-vitelline product—developed by the cells of the follicular epithelium (No. 47). Other protective structures may lie outside the egg-capsule proper, such as the mucous layer in *Perca fluviatilis*, the gelatinous matter surrounding the floating ova of *Lophius piscatorius*, and others, but they are probably ovarian, oviducal, or other secretions, and do not belong to the ovum proper. Further, it seems most in accord with present results to regard the external capsule as a single membrane—variously styled Eikapsel (Müller, His, &c.), Eihaut (Kupffer), Chorion (Lereboullet), Ectosac (Owen), outer yelk-sac (Ransom), and zona radiata (Waldeyer). G. Brook, again, describes in *Trachinus* a thin membrane (his vitelline membrane) outside the zona. Such has not been seen in any of our pelagic eggs. It is generally hyaline, tough, and slightly resilient, and varies in thickness in different species—thus approximately in

Anarrhichas lupus, it is	·00143 to ·00162 in.	*Gadus merlangus*, it is	·000310 in.
Gastrosteus spinachia, „	·0015 „	*Pleuronectes flesus*, „	·000125 „
Gadus morrhua, „	·000312 „	„ *limanda*, „	·000104 „
„ *aeglefinus*, „	·000440 „	*Trigla gurnardus*, „	·000333 „

In pelagic ova it is so exceedingly thin and translucent that the developmental changes in the germ are visible through the capsule,* yet in demersal ova it is not only denser, but presents in many species marked structural features, such as projecting knobs, filamentous processes, reticulations, and the like, all of which, however, must be looked upon merely as modifications of the single capsular membrane—the zona radiata. It is very thin and transparent in the sprat, the egg of which generally shrivels when put in spirit. The zona usually presents laminæ, which Sars observed and counted in *Gadus morrhua*; but such does not imply the existence of separate layers, for chitinous structures of this kind often show a stratified condition. Ryder could only make out the laminæ

* In undeveloped and dying eggs the growing opacity of the vitelline mass is readily seen. This opacity of the egg-contents André wrongly attributes to the capsule itself, which he says becomes opaque (No. 4, p. 197).

in *Gadus morrhua* after treatment with osmic acid, but in both that and other species they were observed at the St Andrews Laboratory without preparation. As the time approaches for hatching, the capsule (*e.g.*, in *Gadus æglefinus*) often breaks up into flakes like the translucent chitinous secretions (tubes) of Annelids. The continued action of water and other causes seems to produce this physical change, so that the embryo is more readily extruded.

We shall glance first at a few of the prominent features of demersal ova—the two most obvious points as compared with pelagic eggs being (1) the greater density of the zona radiata; (2) the tendency to adhere together in masses by reason of the peculiar secretion which issues from the oviduct along with the ova. One of us has pointed out,* that in adhering together, eggs such as those of *Cottus* and *Cyclopterus* (*vide* Pl. I. figs. 1–4) do so by limited areas of their surface, *i.e.*, by facets, and thus the mass of ova is traversed by an intricate system of channels, which ensures more perfect aeration in the circumstances in which they are placed, *e.g.*, in rock-pools. In the slow-running tanks of the Laboratory, however, these eggs develop less successfully than detached and floating forms, since the decomposition of a few frequently causes the death of the whole mass.

Considerable variations are presented by the external surface of the zona radiata. Thus in *Lepadogaster bimaculatus* the capsule shows very evident punctures, and the ova, instead of being fixed to each other, are attached separately to shells, stones, and similar structures. *Anarrhichas lupus*, again, has the largest non-pelagic egg known to us. During the investigations for H.M. Trawling Commission in 1884, one of us had been familiar with the ovarian eggs of this form in their earlier stages, and in a morbid ovary some of the fully developed eggs were retained so late as the month of February, the spawning period apparently extending over the late autumnal or winter season, probably from October or November to December. It was not until the 16th of January 1886, however, that normal mature ova were obtained. A local trawler procured in comparatively shallow water (5 to 6 fathoms) a large mass of them. These ova (Pl. XX. figs. 6, 7) are of a pale straw colour, with a slight opalescent hue. In shape they are more or less spherical, and measure 5·5 or 6 mm. in diameter. The zona radiata presents a comparatively smooth, though minutely punctured appearance (Pl. XX. fig. 8), and is very tough, so that the eggs, which are fixed to each other in the usual manner to facilitate aeration, can only be torn asunder with difficulty. In section (Pl. I. fig. 25) a stratum (*a*), marked by a deep hæmatoxylin-stain, separates an outer thicker from an inner thinner portion of the zona radiata. Fine striations or pore-canals are also seen traversing the entire thickness of the capsule. A single large oil-globule 1·75 mm. in diameter occurs in each ovum. This, as usual, constantly passes to the upper pole, just as the oil-globule does in pelagic eggs. Only a single unimpregnated egg was available for the demonstration of the early condition. In some unhealthy or dying eggs a number of very small oil-globules were seen clustering round the edge

* M'Intosh, *Nature*, June 1886.

of the germ, the general size being about $\frac{1}{300}$ inch. Towards the period of hatching the chitinous zona radiata is more easily torn, and readily splits into lamellæ, all of which show minute punctures (Pl. XX. fig. 8), appearing like minute pale specks on a dark ground. In some again the punctures are lost in a general granular area. Whether these so-called punctures were actual canals, or only radiating striæ, could not be demonstrated.

This separability of the capsule into layers in the later stages does not conflict with the view that it is really a single coat. Such chitinous formations in other forms show the same tendency to split into filmy strata under certain circumstances, and, as explained, a like tendency is exhibited in the extremely thin zona radiata of *Gadus morrhua* and *G. æglefinus*. In size the ovum of *Anarrhichas** resembles that of the salmon (Pl. XX. figs. 9, 10), though the punctures in the latter form (fig. 11) seem to be somewhat larger.

Liparis montagui.—The capsule presents externally a minutely areolate appearance (Pl. I. fig. 4) due to slight elevations, resembling indeed the surface of grained morocco leather, the elevations having a more or less marked linear disposition. In newly deposited examples, or in ripe ovarian ova, the external configuration shows an almost regular hexagonal character (Pl. I. figs. 21, 22), the sutures being pale, while the central regions are more opaque, probably from increased thickness. After exposure to water a change seems to occur, the hexagonal facets becoming less marked, while a series of elevations become visible, and are apparently due, therefore, to a later modification. In oblique views the capsule shows undulating surface-markings (Pl. I. fig. 22). As these ova were not actually observed to be deposited by this species, however, it must be added that a margin of doubt exists as to the feature described.

In this as in other species the zona radiata is at first soft and pliant, hardening subsequently, as in those deposited in the Laboratory. In the fresh condition minute punctures are visible, though these are less distinctly seen after mounting in certain media, *e.g.*, Farrant's solution, and on tearing the capsule the same dense series of laminæ can be separated as in *Anarrhichas* and *Cottus*. While in the ovary the eggs have a pale straw colour, and measure about ·043 inch, the oil-globule being ·0083 or less, but those just deposited in the tanks show a slight increase in size, viz., ·045 inch in diameter, and the oil-globule varies from ·005 to ·0116 of an inch. The eggs of this species are very frequent on sea-weeds, zoophytes, and fragments of sticks and débris at the bottom, in comparatively shallow water as well as in the deeper parts, and they show much variation in colour, from pale straw to a light pink or flesh colour. They have often been mistaken for the eggs of the herring, from which they differ in regard to the structure of the zona radiata, and in the absence of the so-called vitelline membrane, which Mr Brook, however, says is not present. The embryos again are sufficiently diagnostic, for the

* It is remarkable that the masses of the eggs of this species have hitherto escaped observation, fishermen being so little acquainted with them that they were mistaken for those of the salmon. Some time afterwards the recently hatched embryos (then unknown) were recognised by one of us in Edinburgh, having been forwarded to the Fishery Board for Scotland by one of the steam trawlers of the General Fishing Company, Granton.

elongated and somewhat feeble herring cannot be confounded with the shorter and more vividly tinted larval sucker, which shoots into the surrounding water at once on issuing from the egg. The ova usually referred to this species, however, require further study, and the condition of the larva on emergence presents certain differences in the several varieties. It is possible that several species have similar ova, but where absolute certainty in regard to their determination was not possible, only those having the same size and structure were grouped under the head of this species. The spawning period ranges apparently from January to June.

Cyclopterus lumpus.—The ova of this species are very variable in colour, ranging from a beautiful amethystine lustre through the various shades of straw-tint to greenish. The zona radiata is thick, and minutely punctured, but presents no special thickenings or superficial wrinkles, except where the facets of attachment are situated. The eggs are fixed together in sponge-like masses, so as to permit free aeration, yet the hatching of this species in confined tanks is somewhat difficult. The germ, as in pelagic forms, keeps for the most part at the lower pole, the oil-globules ascending to the upper pole. Their diameter is about ·1 inch, while that of the large oil-globules is about ·041 and less.

Ova, apparently of this species, were obtained in great quantity from the stomachs of codling off Boarhills (Fifeshire), but, unless erroneously diagnosed, the gastric juice had caused a diminution in diameter, as they measured only ·083 of an inch, while the large oil-globule in each measured ·026, and one or two smaller globules were also present. Though to a slight extent digested, this ovum showed much resemblance to that of *Cyclopterus*, and formed masses of a yellowish green colour. In addition to the ordinary punctate structure, the zona agrees with that of *Cottus* in presenting larger, more evident dots at intervals (Pl. I. fig. 24); indeed, this arrangement of larger punctures in the midst of the smaller ones is more distinct than in *Cottus*. They resemble large canals rather than radial striæ, and they are finely dotted when viewed in profile, as at the edge of a torn fragment. It is noteworthy that at the same period as the above partially digested ova were obtained, a considerable quantity of similar eggs of a pale straw colour were procured on the beach near the Laboratory. Their diameter was ·0916 and that of the large oil-globule ·031, and several smaller globules were also present. The ordinary pores were larger than in *Cottus*, but the larger pores, scattered at intervals, were similar. If these be the ova of *Cyclopterus*, which they closely resemble, considerable latitude must be given in regard to diameter. It has, however, to be borne in mind that the condition of the ova (*i.e.*, whether they had been subjected to dessication or otherwise) was unknown. The spawning period of *Cyclopterus* extends from February to the end of May, and occasionally even a little later.

Agonus cataphractus.—The ovaries of a number of female specimens caught by the sprat-nets in the estuary of the Tay were found to show nearly ripe eggs in December. The eggs are large, and of a dull golden or dull yellow colour, their diameter being ·07 inch and that of the oil-globule about ·0216. The zona is minutely dotted with punctures arranged in a linear series. The surface is also covered with well-marked areolæ. (Pl. I.

fig. 23). This species seems to spawn from January (or perhaps even from December) to April.

Cottus scorpius (Pl. I. fig. 3).—The ova present various shades of red, inclining at times to orange or yellow. Their diameter averages ·075 inch, and the large oil-globule ranges from ·015 inch in diameter downward. The zona is smooth, except where the facets for attachment to adjacent ova occur. Minute dots are visible under a high power, and these have a more regular linear arrangement, as a rule, than in *Cyclopterus*. Moreover, larger dots occur at intervals all over the surface, recalling those noted in *Cyclopterus* taken from the stomach of young cod. In the Report to H.M. Trawling Commission,* one of us has alluded to the error of Professor Alexander Agassiz in considering the ova of *Cottus* pelagic, a fact overlooked by Mr Cunningham.†

Ammodytes tobianus, L.—G. O. Sars states that the comparatively large ova of this species are not pelagic, but are laid in loose sand, where they go through their development. Couch, again (No. 44, iii. p. 138), considered that it sheds its ova in this country as it dashes through the sand in December; while Day (No. 51, i. p. 333) found the reproductive organs in both male and female, at St Ives, far advanced in August and September. On the other hand, Thompson states that in Ireland they were nearly ripe at the end of July. The organs, however, were found to be small in November at St Andrews. Early in May some specimens (none more than 6 inches in length) showed ripe spermatozoa, though the testes were comparatively small; while in the females the ovaries were not much developed, and contained very minute eggs. These eggs were transparent and granular, with a large germinal vesicle. Some larger eggs, five or six times the diameter of the remainder, showed a coarsely granular yolk, with many small oil-globules, and a very thin external capsule, which is finely reticulated, and provided with minute punctures as in other forms. In the ovary the eggs appear to have a somewhat whorled arrangement. Later, about the beginning of June, the reproductive organs in about twenty examples showed an irregular state of advancement, some having fairly advanced ovaries, while others were rudimentary. In those best developed the ova were of a rich orange colour, "reddish yellow," as Sars said, and they were just visible to the naked eye as minute grains $\frac{1}{75}$ of an inch in diameter. The germinal vesicle was still very evident, measuring $\frac{1}{200}$ inch. Most of the larger ova were of this size, though others were much smaller, the smallest being in fact less than the nucleus of the largest eggs, and their nuclei showed many nucleoli. The zona is distinctly dotted at this stage. The sperms in the male fishes showed a distinct head, but no motion was visible at this time. So far as could be observed at St Andrews, the spawning period of this species would seem to be late, indeed so late as to bring it within a reasonable distance of the pelagic larval forms described in a subsequent chapter.‡ In some examples, however, examined in the middle of December, the genital

* 1884. † *Op. cit.*, p. 103.

‡ Section xi. Investigations, at present being carried out by Mr W. L. Calderwood at the St Andrews Laboratory, may clear up the subject.

organs were so little developed as to form two rounded cords. From the fact that no definite series of pelagic ova has been found previous to the appearance of the larval forms, the ova would appear to be demersal.

Gobius ruthensparri.—In a female specimen about 3 inches long, obtained on 25th January 1886, the ovaries were found to be small, though the ova were sufficiently developed to be visible to the naked eye. Under the microscope, ova of various stages were seen, the largest being about a line in diameter. A germinal vesicle was present, and the central region of the egg was filled with well-marked globules (yolk).

Centronotus gunnellus.—Like *Zoarces viviparus*, this species is characterised by the presence of a single unpaired reproductive mass in the form of a median band between the intestine and the abdominal roof. Unlike *Zoarces*, however, the male organ of the gunnel is also unpaired. In DAY's recent work on British Fishes the following note upon the spawning of this species occurs (No. 51, vol. i. p. 210):—"NILSSON states that its spawn is deposited in November. Mr PEACH, however, in June believed he discovered the spawn of this fish in Fowey, in Cornwall." At St Andrews, where it is abundant, frequent examination of the reproductive organs supports NILSSON's observations. In the earlier part of the year (February) the ovaries of the female are very slightly developed, minute ova at various stages occurring in the follicles. In May the male elements are less prominent than the female, for the ovary is the larger organ. In many the structure is in a state of degeneration, large fatty globules and other granules taking the place of the sexual elements. The ova at this time still show great variation in size, the germinal vesicle being also present and unaltered. Towards the end of November females, though of small size, present a large, clavate ovary, tapering from the liver in front to a point behind the anus. The ova are now readily seen by the naked eye, and those on the surface are of nearly uniform size, viz., about ·043 in diameter. Several oil-globules (·012 in diameter) occur in the larger ova, and the yolk is opaque on account of the abundant straw-coloured, almost opaline, yolk-spherules. Outside the ovary is a transparent membrane, apparently continuous with the interstitial connective tissue, and not readily removed from the surface. The smaller ova are finely granular, and in some (the larger) small oil-globules are present.

The ova of this species after deposition seem to have been first observed by Mr ANDERSON SMITH,* a member of the Fishery Board for Scotland. He found them, probably on the west coast, from February to April. At St Andrews they have hitherto been obtained amongst the rocks in March, masses about the size of a walnut (as Mr SMITH states) occurring in the holes of *Pholas*, the adults in each case being coiled beside them. The ova adhere together like those of *Cottus* or *Clupea harengus*, and have a diameter of ·076 inch, while the oil-globule measures ·0166 to ·016 inch. In those nearly ready to hatch the zona radiata is somewhat tender, and presents the usual laminated appearance. It is also most finely and regularly punctate, after the fashion of wire-cloth of great tenuity. The ragged margins especially exhibit the

* Quoted by Mr CUNNINGHAM, *op. cit.*, p. 125.

appearance of finely crossed fibres, partly due in all probability to the breaking up of the tissue.

Blennius pholis.—In May a large male, $6\frac{3}{4}$ inches long, was procured at the East Rocks, St Andrews. The testes were highly developed, and almost reptilian or amphibian in appearance. They form two large flattened organs, or rather are rounded anteriorly, and flattened on the inner side—the two bodies, in fact, being precisely like the two separated halves of a long bean. The blood-vessels run along the flat surface, and give off branches which spring as it were from a midrib. In colour they are of a faint pinkish white. The outer or convex region is of a firmer texture and more translucent than other parts of the testis, being composed apparently of tubules containing spermatozoa in full activity and abundant sperm-cells. The whiter opaque region consists of aggregated sperm-sacs. The spermatic duct leading to the genital aperture is exceedingly wide, and on one side shows a spermathecal enlargement, which, at first sight, resembles an additional urinary bladder. The ducts open by an aperture on a prominent papilla behind the large corrugated anal orifice. This strong papilliform protuberance approaches that in fishes which are known to copulate, but there is no account of such in this species. A little later (viz., on the 23rd June) an adult female, 5 inches long, had the ovaries much enlarged—containing a mass of large bluish-grey ova, and smaller ones of a slightly orange hue. The minute structure of these somewhat peculiar ova has been carefully described by Dr Scharff.* The ova (which were not quite mature) measured about ·0415 of an inch in diameter.

The above facts show that this species deposits its eggs apparently during the early summer; Parnell, indeed, names the month of June, while Dunn considers that it spawns in spring. Couch states that it deposits the ova on the roof of small caverns in rocks near shore (*Zool.*, 1846, p. 1419); and Day, who quotes the above authors, adds that he found minute fry at Penzance in August. At St Andrews young specimens, about an inch long, and which had acquired the features of the adult, are abundant in the pools of the East Rocks about the middle of September.

Blenniops ascanii.—On 14th June 1886 a fine male, procured in a crab-pot off the Buddo Rock, Fife, showed testes only partially developed. The stomach was distended by eggs of *Cyclopterus*, upon which it had been feeding largely.

A female in August exhibited only traces of ova—the ovaries being apparently atrophied, but on the 16th September both organs were very large, the individual ova reaching about $\frac{1}{18}$ inch in diameter.

Motella mustela.—On 17th July 1885, a female rockling, 6 inches long, was examined, and the ovaries were found to be connate posteriorly, and contained ova of some size, so that the species must pair very early in winter, and the spawning period would seem to be very lengthened. In May the tanks in the Laboratory were found to be full of the floating ova of this species, and during March, April, and May the ripe eggs appear usually to be ready for extrusion, so that the ova of the female above referred

* *Proc. Roy. Soc.*, vol. xli. (1886) p. 449; and *Quart. Jour. Micr. Sci.*, Aug. 1887.

to, in which the unripe ova were of variable size, large and small, would probably have been retained until the end of winter or beginning of the year. The pelagic ova of this species are amongst the most abundant forms in and beyond the bay in March, April, and May.

We have already spoken of the capsule as a zona radiata—a protective membrane of general occurrence in the ova of most diverse groups of Vertebrates. Thus in the Aves a zona radiata is present, though it does not persist; but at an early stage it disappears, and the egg leaves the ovarian follicle enveloped by another membrane which is distinguished as the vitelline membrane. This second membrane is exceedingly attenuate, so that it is difficult to distinguish it from the outermost layer of yolk-cells from which it is derived. The *Reptilia* possess also two membranes; but, unlike the birds, they are not both of vitelline origin, the outer, which is very thin, EIMER (No. 53, p. 418) declares to be a product of the follicular epithelium, and therefore chorionic; but the inner is thicker, and vitelline in origin; and EIMER regards this as the zona radiata (his zona pellucida). The capsule in the *Amphibia* (Rana) is a remarkable structure, and would appear to be really a chorio-vitelline membrane, for the inner cells of the ovarian follicle form a layer very closely applied to the true vitelline membrane, and as the latter becomes continuously thinner the two layers are really inseparable, and form one layer, of which the outer stratum is chorionic, and the inner one is vitelline.

In the Elasmobranchs a double layer is present, the outer being first formed, and regarded by BALFOUR as vitelline; while the inner one, equally of vitelline origin, he distinguished as the zona radiata. Both, however, atrophy as a rule before the egg leaves the follicle. In Cyclostomes (*Petromyzon*) two layers are described, an outer imperforate, and an inner perforated layer. The outer layer on contact with water swells up and forms a gelatinous coating by which the eggs adhere to external objects. In *Myxine*, according to J. T. CUNNINGHAM'S researches, the thick capsule is a chorion, being developed along with its solid projecting processes from the follicular cells. Possibly a delicate vitelline membrane may be developed internal to the outer homogeneous capsule, but this Mr CUNNINGHAM was not able to decide (No. 46, p. 600). Notwithstanding that a double egg-membrane is so common, as indeed KÖLLIKER long ago pointed out (No. 80, p. 84), yet in the Teleostei the recognition of a single layer of vitelline origin accords best with the character of the capsule in general, in the mature ovum.* Certainly LEREBOULLET'S designation "chorion" (No. 93, p. 459) is inappropriate;† nor does KUPFFER'S view, that the capsule in certain osseous fishes is double, like the Elasmobranchs, seem better justified. KUPFFER holds that, in the case of *Clupea*

* Dr MARTIN BARRY affirmed that one membrane only envelops the ovum in fishes, no layer being formed external to the vitelline membrane (No. 21, p. 309). SOLGER also came to the same conclusion from an examination of *Leuciscus rutilus* (*Arch. f. Mik. Anat.*, 1885).

† LEREBOULLET, however, later in the same treatise, refers to the chorion as of vitelline origin, and "produced by the primitive vitelline membrane separated from the vitellus" (No. 93, p. 507).

harengus, two separate layers, an outer vitelline membrane, and an inner zona radiata, may be distinguished (No. 87, p. 178); but HOFFMAN does not think the distinction justifiable—one membrane alone being present, which, however, presents an inner less-defined part, probably more recently formed, or in course of formation, from the vitelline cortex; and G. BROOK supports this interpretation (No. 34*a*, p. 201).* If the outer concentrically-laminated stratum be regarded as a layer separate from the inner stratum which shows radial striations, then with KUPFFER we must consider the former as of exceptional occurrence amongst Teleosteans (No. 87, p. 178). BROCK, again, figures two Teleostean ova with double capsules, the outer layer being striated in one case and unstriated in the other (No. 29, Taf. xxviii. fig. 7, *f.*; Taf. xxix. fig. 6, *b*, *c*). The interpretation as a single layer, we repeat, seems, however, better founded, for if the ovum of *Callionymus lyra* be examined, we find external to the zona radiata, which has the usual structure, "a series, for the most part, of hexagonal reticulations like those of a honeycomb," not unlike the reticulation of the early ovum of *Ammodytes tobianus*. "These spaces are not quite uniform in size, but many are. Some again have four, six, or seven sides; . . . . the septa bounding the reticulations stand out very distinctly, and their edges show minute striæ" (No. 106, p. 481, also Pl. xiii. figs. 1, 2, 3, 4). The ripe ova of this species have been examined at the Marine Laboratory, and the reticulation in both cases is external, and is evidently inseparable from the zona radiata. The same condition would appear to be present in the pelagic ova of *Crenilabrus tinca*, recently described by J. H. LIST, the outer part of the zona consisting of regular six-sided areas, and the inner only of fine parallel striations.† Such elaborate modifications of this single layer are probably illustrated by the ovum of *Cyprinus dolbula*, with its radially directed rod-like processes; of *Perca fluviatilis* (No. 111, p. 186), with its prominent hollow cylindrical appendages, which interlace, and, with the mucous envelope, hold the eggs together in "élégants réseaux," as LEREBOULLET describes (No. 93, p. 471); but they do not serve, as the same author states, for absorption like the minute canals, though both structures penetrate the capsule. In such forms also as *Blennius*, *Gobius*, and pelagic eggs like *Heliasis* and *Belone*, long filaments occur near the micropyle, and are pronounced by HOFFMAN, who describes them, as simply excrescences of the zona radiata. If we regard the capsule in Teleosteans as essentially a single layer, then the dissimilarity of the elaborately modified capsules of the foregoing species —of the less complex capsule in *Clupea harengus* (No. 87, p. 178), and in *Esox lucius* (No. 93, p. 465); and of the extremely simple membrane in the ova of Gadoids, Pleuronectidæ, and others, wholly disappears. The species in which various layers, not to say distinct membranes, have been described, find their place in the same category as the ova of the cod and like forms with simple layers. That the capsule can undergo elaborate modification is easily understood, when it is noted that in its early condition it is always

* See also LEREBOULLET'S description of a similar inner layer closely applied to the yolk in the pike, the outer stratum being alone striated (No. 93, p. 465).

† *Zeitsch. f. wiss. Zool.*, Bd. xlv. (1887) p. 596, fig. 1, *a*, *b*.

soft and pliant, and may remain so even after deposition, as we find to be the case, notably in the thick capsules of *Gastrosteus spinachia* and *Cottus*. These ova, for some time after deposition, are soft and yielding, possessing, as Prof. Allen Thomson (No. 153) states, in the fresh-water congener of the former, "so little elasticity that it usually retains dimples or impressions made upon it from without." In this connection it may be mentioned that the so-called outer layer in *Clupea harengus* is slightly facetted (No. 87, p. 177), this being due, doubtless, to the impress of the follicle-cells before the egg is extruded—a suggestion which may also be applied to the similar appearance in the case of *Perca* (No. 111, p. 187). The zona radiata, as its name implies, has a characteristic radiate structure in many Teleosteans. The real nature of the striation so visible in section has been much disputed, and there is little unanimity of opinion in regard to it. In many species this feature has not yet been made out, *e.g.*, in a number of familiar Gadoids, viz., *G. merlangus*, *G. æglefinus*, *G. luscus*, *Molva vulgaris*, and some of the Pleuronectidæ, such as *P. flesus* and *P. limanda*. The capsule in the familiar Pleuronectid, *Pleuronectes platessa*, again, is very distinctly punctured (Pl. I. fig. 20). Cunningham has recently mentioned that the zona radiata of the cod usually described as not punctured (*vide* Ryder, No. 141, p. 457), exhibits pore-canals, but he does not describe them in the ovum of *Trigla gurnardus;* yet the latter, so far as our experience goes, shows them much more distinctly than those of the cod; indeed, we have not yet satisfied ourselves concerning the latter. In the ovum of *Trigla* one of us has demonstrated that the whole surface of the capsule is minutely and faintly dotted (Pl. I. fig. 19). This punctate appearance is especially distinct after the escape of the embryo. The capsule of this form in the unimpregnated condition shows numerous wrinkles—the yolk occupying a comparatively small area, so that a large perivitelline space exists, which, however, diminishes after fertilisation, until the vitelline globe almost fills the capsule, which at the same time becomes less distinctly wrinkled. The corrugation of the zona radiata is, however, a characteristic feature, and exists in all the eggs of this species. The zona is firm and elastic to a remarkable degree for a pelagic form, and its unevenness causes some obscurity—only a faint line of dots being as a rule visible along the ridge which happens to come into focus under the microscope. In one instance the zona presented a series of scale-like markings or areolæ (Pl. I. fig. 16), probably due to an unusual or morbid condition in connection with the follicular epithelium. The normal wrinkles (seen best in *T. gurnardus*) also occur in the lemon-dab (Pl. I. fig. 18); and Ryder speaks of these in *G. morrhua* as fine lines crossing each other at definite angles. Such lines, however, are less visible in eggs which are healthy and perfectly mature. The typical zona radiata exhibits, as Von Baer discovered in Cyprinoids, fine striations perpendicular to the superficies of the yolk, and Carl Vogt described at greater length the same feature in the Salmonidæ (No. 155, p. 7); while Reichert noted it in the ova of *Tinca vulgaris* and *Leuciscus erythrophthalmus*, and Leydig in *Gobius fluviatilis*.

Are these striæ really canals, or merely fine fibrillations, such as we find in the transient zona radiata of the fowl under a high power? In either case a punctured or

dotted appearance would be produced superficially, as in a large number of Teleostean eggs, especially in the comparatively dense capsules of fresh-water forms. These punctures may be comparatively large and distinct, as described by MÜLLER in *Perca* (No. 111, p. 187–8), and by LEUCKART in *Esox;* or they may be of smaller size, as in *Salmo fario* (No. 153, p. 101, and fig. 68, c, d), *Gastrosteus spinachia;* or of extremely minute size, as in certain pelagic forms, *e.g.*, *Trigla gurnardus* and *P. platessa.* Frequently the striations are observed to pass only partially through the capsule, and the outer stratum is then imperforate, instances of this condition being the capsule of *Clupea* (No. 87, p. 177), and *Esox* (Aubert), *Gastrosteus spinachia*, and probably *Trigla gurnardus.* In other ova they traverse the whole thickness of the capsule, as is the case in *Salmo fario* (No. 4, p. 198), and in *Perca fluviatilis*, according to the experiments of J. MÜLLER (No. 111, p. 188). The distinguished observer just named was convinced that, when he placed the eggs of the perch under pressure, oily matter from the interior of the egg could be squeezed through the canals of the zona radiata, and the canalicular structure of this membrane would appear to be demonstrated in this instance. Other observers, however, strenuously deny this, and, like ANDRÉ, pronounce the so-called canals to be nothing more than rectilinear striations directed radially from the inner to the outer surface of the capsule (No. 4, p. 202), precisely like the radial fibrillations in the zona of the fowl's ovum. It is only necessary to observe the effect of desiccation on the egg of the cod, and then the action of water, to prove that a ready interchange occurs through the *zona* either by pores or by ordinary endosmose.

Little can be said here as to the origin and growth of the zona radiata, for its development is already complete when the ovum reaches maturity. That it is a true vitelline membrane admits of little doubt; and HOFFMAN'S opinion, that it is secreted by the vitelline mass as a superficial layer during the intra-ovarian period, and is not separated until it shows an appreciable density and firmness, is probably well founded.* RANSOM holds that, after it is defined as an external membrane, it continues to grow interstitially up to a certain stage, when growth ceases, and it performs a solely protective function (No. 127, p. 494). Other layers are formed later upon the surface of the yolk after the zona radiata has become detached as an elastic protective capsule, and these may claim to be called vitelline membranes, as indeed they have been styled by various authors. Thus, OELLACHER, when speaking of the vitelline membrane in the trout (No. 113), really means the stratum of germinal protoplasm, the polar segregation of which forms the blastodisc; while LEREBOULLET uses the same term for the layer of protoplasm which ventrally limits the intestinal tract of the embryonic fish at a comparatively late stage (No. 93, p. 612). Such uses of the term "vitelline membrane" for very different layers (though all of vitelline origin) are not to be approved, and the name zona radiata is at once distinctive and appropriate for that vitelline membrane

* The development of the vitelline membrane in *Triton* has been shown in an interesting manner by Mr IWAKAWA, and his descriptions and admirable figures (see No. 75, p. 274, and pl. xxiv. figs. 24–26) will apply in the case of the Teleostean capsule.

which forms the external capsule, and subserves a protective function. When the embryo is sufficiently mature the capsule is burst,—the rupture being due, no doubt, to the vigorous motions of the young fish, which in the case of *Pleuronectes flesus* generally emerges from the capsule by pushing out its tail.

The Micropyle.—The zona radiata is pierced by the micropyle (Pl. II. fig. 19, *mic.*), an aperture probably universally present in Teleostean eggs, and in these it varies very little in structure and appearance. Thus in the salmon, trout, pike, ruff, perch, bullhead, gudgeon, minnow, chub, and various species of *Gastrosteus*, Ransom's description accords almost perfectly with the micropyle, as seen in the cod, haddock, ling, whiting, bib, flounder, dab, plaice, gurnard, and others. At a certain point the capsule is distinctly thickened, and an internal conical elevation is formed, which, as Balfour says (No. 10, p. 51), corresponds with an external funnel-like depression, while a cylindrical canal connects the bottom of the funnel with the apex of the inner papilla.* The thickened appearance of the capsule in the micropylar region is not produced simply by the protruding hillock, and due to the crateriform depression outside; but as André (No. 4, p. 201) ascertained, and as may be easily demonstrated in the delicate translucent ova of the Gadidæ or Pleuronectidæ, the capsule is actually thicker at this point (Pl. X. fig. 9). List shows the same feature in *Crenilabrus tinca*.† Viewed from above, three parts may be distinguished—a large outer annulus and a smaller inner ring, with a central pore which is the opening of a cylindrical tube. In the trout these measure, according to André, ·015 mm., ·008 mm., and ·005 mm. in diameter respectively. The first-named ring is the rim of the external crater; the inner ring marks the narrower, deeper portion; while the central aperture is the essential part, the true micrOlpyar canal, which is not, however, perfectly cylindrical, but midway along its course distinctly enlarges, and then narrows again. This sinuosity observable in the canal proper, André thinks, is produced by the ends of the pore-canals or radial striæ which jut out slightly into the lumen of the micropyle (No. 4, p. 201). That the micropyle is really a depression, and not simply a puncture, is shown by the fact that the striations of the zona radiata present an inclination towards the micropyle, which is increased as the aperture is approached, and still more so down the walls of the crater, their outer ends being directed towards the cavity of the depression, and forming projections into it as just stated.

This inclination of the striæ is shown by Ransom and others; but His does not indicate it in his figures of the ovum of *Salmo fario* and *S. salar* (*vide* No. 67, Taf. i. figs. 7, 8, 9, and 10); and the same may be said of List in his recent paper. Connected with the depression and thickening of the capsule around the micropyle, is the striking appearance external to the larger annulus seen in the marine and fresh-water species of *Gastrosteus*, where bold radiating striæ pass away from the margin of the external crater (*vide* Nos. 153 and 67, Taf. i. fig. 15), a feature less marked in the chub, in which the margin

* Ransom speaks in *Gastrosteus* of the micropyle as projecting actually into the protoplasmic disc, and of a subsequent shortening of its funnel after fertilisation (No. 127, p. 450).

† *Op. cit.*, p. 597, fig. 2, *a*.

is crenate and the sides are furrowed. In the pike Ransom describes the micropyle as trumpet-shaped, and projecting slightly from the surface of the capsule (No. 127, pl. xvi. fig. 25, *a*); while in the minnow, too, the margin is raised around the outer opening of the funnel (*Ibid.*, p. 456). Striæ are occasionally seen in certain pelagic forms, *e.g.*, in *Trigla gurnardus* and *Gadus æglefinus*, but the margin of the crater is usually sharply marked, and the aperture itself very clearly defined without radial markings. When viewed in "full face," the funnel seems larger than it really is on account of the torsion, so to speak, of the zona radiata, which appears as if bent in to form the orifice, a feature André particularly points out (No. 4, p. 199), and to which we have made reference above.

The micropyle thus varies in appearance. Usually the external opening is the larger; but in some cases this is reversed, a large gaping internal opening being present (*vide* fig. of ovum of *G. æglefinus*, Pl. I. fig. 14), while the external orifice is small. The striations above mentioned are also visible in this case—the whole peri-micropylar region being granular, while the granules have a tendency to range themselves in radial lines. Near the micropyle in some examples an accessory structure is present, due apparently to a granular protrusion of the zona (Pl. I. figs. 11 and 15). In this and other cases the micropyle was distant from the germinal area. Fertilisation in pelagic eggs does not produce any marked change in the micropyle, certainly none like that described by Ransom, and just mentioned. In one instance, beside the micropyle proper, was a depression plugged by an ovoid granular structure, while a large group of "oleaginous" spheres lay upon the yolk near the micropyle (Pl. I. fig. 17).

Origin, Position, and Function of the Micropyle.—The mode of origin of the Teleostean micropyle is unknown. When first observed in the mature ovum it presents the features maintained throughout the subsequent history of the egg. Leydig describes (No. 97, p. 376, fig. 6) the earliest ovarian egg of *Trigla hirundo* as somewhat pyriform and stipitate, recalling, in fact, the stalked ovum of *Unio*, in which the micropyle marks the pedicular point of attachment by which the egg adheres to the ovarian capsule, as Carus was the first to note. Such an interpretation of the micropyle, as the cicatricule left by a pedicle, cannot in the case of the osseous fishes be adopted, and we are still left in doubt as to the way in which the aperture arises.

It is interesting to observe that in many forms the position of the micropyle is constant, and corresponds to the germinal pole, where the embryonic area is formed, as, indeed, Ransom found in *Gastrosteus*. In *Perca*, however, the aperture is turned towards the inside of the egg-tube—the ova being fixed in a cylindrical mass, so that the possibility of the micropyle being blocked up by adjacent ova is obviated (No. 127, p. 456). Gerbe similarly says, "that the micropyle plays an important part, as the disc always collects near the place occupied by it" (No. 57, p. 330). Neither Ransom nor Gerbe examined pelagic ova; but from the later observations of Ewart and Brook, it would appear that in floating eggs the micropyle is always found in the lower hemisphere (No. 55, p. 55). This position is, of course, the reverse of that in stationary demersal ova, in which a preformed disc is commonly found in the upper (animal) segment; whereas in

pelagic eggs the blastodisc formed after fertilisation is also theoretically constant, but in the reverse segment—the animal pole being underneath, and in calm water the germ is usually found at this lower pole.*

As to the function of the micropyle, most authorities are agreed that it is connected with the fertilisation of the ovum, affording means, in fact, for the entrance of the spermatozoa. Kupffer, however, calls this generally adopted view into question, and doubts whether it has any essential part to play in fecundation (No. 87, p. 179). In the ova of lower forms the function named has been universally admitted from the time Meissner first described the aperture in crustaceans and insects (No. 102, p. 272), and Leuckart laboriously worked at the structure and function of this aperture in a large variety of insects. The latter, in his elaborate paper, states that he beheld sperms not only adhering to the outside of the egg, but entering the micropyle; and indeed figures this phenomenon in the ovum of *Melophagus ovinus*, a crowd of spermatozoa being collected at the external opening, though not more than three or four find entrance. In Teleosteans its function appears to be solely that of affording ingress for the fertilising element, though Ferd. Keber (No. 77) conceives not only this to be the case, but that through it there is an actual outflow of the contents of the egg—the purpose of this outflow being to lubricate the canal and favour the entrance of sperms, as well as to increase the vacant space within for the reception of the spermatozoa.

Meissner, who first described the micropyle in the ovum of the rabbit, thought that the aperture only penetrated the vitelline membrane, and that it was effectually closed over by the chorion outside (No. 103). A modified view has been put forward by Ransom, who was probably the earliest to discern and rightly interpret this aperture in osseous fishes.† He was of opinion that a delicate film covered the micropyle, which was only ruptured by the entrance of sperms; and more recently Boeck, in connection with his remarkable theory of osmotic fertilisation, to which we shall refer shortly, conjectures that a clear membrane, in the case of *Clupea harengus*, closes the aperture of the micropyle (No. 23, pp. 5, 6). Besides admitting sperms, a small quantity of water may also enter, which (water) mingles with certain organic particles, and fills up the space between the vitellus and the zona radiata in the extruded ovum.

The Deutoplasm or Food-Yolk.

Within the egg-capsule is the ovum proper, a spherical translucent mass, largely composed of fluid food-yolk. With the food-yolk, which serves for nutrition, there is interfused active protoplasm, and this, at an early stage, collects as a delicate film over the surface of the yolk-ball; indeed the mature ovum of Teleosteans, before fertilisation, exhibits a distinct superficial layer of clear protoplasm, in which minute vesicles and oil-

* According to Ryder, the germ is lateral in *Alosa*.

† Bruch independently discovered the micropyle in the eggs of the trout and salmon (No. 35, p. 172).

spheres are embedded.* During the first hour after fertilisation these translucent vesicles are readily seen under a moderate power (450). Occasionally granular protoplasm is observed at certain parts of the contour of the vitellus in the haddock. A similar appearance occurs in the cod, in ova which are abnormal though still translucent. Amongst these vesicles are others extremely minute and very numerous, which in refracted light have the appearance of punctures.

To distinguish the albuminoid matrix, which forms the greater part of the bulk of the egg, from the active germinal protoplasm, the name "deutoplasm," conferred by Prof. E. VAN BENEDEN, is both appropriate and convenient. This deutoplasm rarely has the appearance of yolk-segments contained in a sponge-like network; but is composed in many pelagic eggs of minute yolk-particles aggregated in a matrix apparently homogeneous, highly refractive, and coagulating on the addition of water. The latter feature has long been known, for LEREBOULLET found coagulation to take place in the ovum of *Salmo fario*, just as VOGT had noted in *Coregonus palæa* (No. 155, p. 11).† Broadly speaking, we may say of the yolk in the Teleostean ovum that it possesses special features of its own, which separate it from the nutritive matter of other vertebrates; whereas the yolk of the Elasmobranchii resembles in a very marked manner that in the Avian egg. There is apparently little difference in the specific gravity in various parts of the deutoplasmic matrix, as it retains any position in which it is placed before the aggregation of a polar disc; but RANSOM questions whether its specific gravity is equal throughout, and thought that nearer the surface it is of a more fluid consistency, or, as he says, "I had some reason to think a little less dense than the centre, as it ran more freely; but all parts flowed from a rupture like very thick syrup" (No. 127, p. 436). The greater density of the deeper deutoplasm can be readily explained by the movement of the interfused protoplasm surface-wards, so that the central part of the yolk-globe becomes more purely yolk-matter, while with the more superficial strata a larger, though constantly diminishing, quantity of germinal protoplasm will still be intermingled. KOWALEWSKY considers that a protoplasmic network must exist in the yolk (*Carassius*, *Polyacanthus*, and *Gobius*), since after hardening the latter presents polygonal partitions (*Zeitsch. f. w. Zool.*, vol. xliii., 1886). He also terms the yolk the entoblast, in contradistinction to the germinal disc or ectoblast.

The freedom with which the so-called oil-globules in various forms (*e.g.*, the gurnard and ling) move through the deutoplasmic globe not only proves its very fluid consistency, probably corresponding with that of thick cream, but shows the absence of a definite

* LEREBOULLET inclines to the opinion that the yolk is active in the formation of germinal protoplasm; "at any rate," he says, "in the Lizard and Bird we find it before the germinal vesicle is ruptured" (No. 95, p. 11).

† The behaviour of the deutoplasm under various conditions was made the subject of some interesting observations by Dr DAVY in the ovum of the charr (*Salmo umbla*), and he found that while contact with water in quantity coagulated it, the careful application of water in minute portions did not do so. Again, when heated even so high as 212° F., it did not coagulate, nor did it under the influence of steam; whereas boiling water at once effected the change, owing, it was inferred, not to the heat, but to the admixture of water. While acids, salts, and alkalies had no coagulating influence, except when dilute, nitric acid, corrosive sublimate, and alcohol produced the change immediately. DAVY came to the conclusion, as a result of his researches, that the deutoplasm of the charr and other Salmonoids has properties distinct from the albumen of the Avian yolk (No. 50, p. 436). Results similar to those of DAVY were obtained by RANSOM in the various Teleostean eggs which he studied (No. 127, p. 436).

protoplasmic network, such as the reptilian ovum presents, or as Dr SCHULTZ demonstrated (No. 144) in the Selachians.

Little or no food-yolk makes its way into the germinal area, so that, as LEREBOULLET observes (No. 93, p. 485), it takes no part in the segmentation of the germ. Indeed, all evidence tends to prove that the deutoplasm is in an inert or quiescent state, and only passively contributes to embryonic development, being slowly incorporated by the active protoplasm of the blastodisc in a mode which RYDER compares to the process of ingestion and assimilation in *Amœba* (No. 141, p. 557).

When the eggs of *Gadus morrhua* are partially dried, the surface of the yolk shows a series of clear reticulations, which on re-immersion in water run together and disappear in the course of eight or ten minutes; such reticulations have, however, no connection with the later protoplasmic reticulation of the vitellus after epibolic extension of the blastoderm, and which is very noticeable in the cod, common dab (Pl. V. figs. 3, 11), and others. HAECKEL regards it as so much passive matter contained in a gastrula-cavity (No. 62); but in Teleosteans it plays a more important rôle in later stages than that of supplying crude pabulum to the germ. Indeed, the germinal protoplasm BALBIANI holds to be solely transformed yolk—not a mere segregation of interfused germinal matter. The germ, he says, is formed "by endogenous development of cells at the expense of the yolk or primordial protoplasm;" but he repeats the error of COSTE that the germinal area is never formed until after fecundation (No. 9).

J. T. CUNNINGHAM, in a highly suggestive paper, observes that the yolk and germ are equally concerned in the processes of cleavage; segmentation in Teleosteans (as in Amphibians), dividing the ovum at the first stage of cleavage not equatorially, as E. VAN BENEDEN holds (No. 25), but meridionally into two similar halves, each with a cap of protoplasm and a mass of subjacent food-matter (No. 48). This view, however, gives to the crude deutoplasm an importance which cannot be accorded to it, even though cleavage as regards the yolk be merely potential and never fully achieved.

The separation of the deutoplasmic mass into a segmenting blastoderm (Pl. XXII. fig. 1, *bd*), and an appended ball of pabulum (*Ibid.*, *y*), is more complete in osseous fishes than in Elasmobranchs, and imparts to the yolk rather an accessory character than that of an active participator in the whole process of cleavage.

That it contributes to the growing organism, and even buds off cells to build up part of the enteric tract, does not conflict with this view, which is supported by the fact that the yolk persists as a bulky appendage on the ventral surface of the young fish (Pl. XIX. figs. 5, 7), until a late embryonic stage, being enclosed by the body-wall, and finally absorbed when the post-larval stage is reached. The passive rôle attributed to the yolk RYDER would confine to the early stages, while later its function, he holds, is more important, since it becomes through the medium of the intermediary layer an active part of the ovum (No. 141, p. 569).

But this view is not inconsistent with that here maintained, for if it serves as pabulum, this is really a part secondary to actual participation in blastodermic cleavage, and while

the transformed substance of the cortex is difficult, if not impossible, to separate from the protoplasm of the germ proper, yet the yolk in the main is neither concerned in the cleavage of the germ proper, nor actively contributes to the increase of the embryonic tissues. In the Gadoids and other forms no vitelline circulation is established, and the absorption of the yolk is a slow and circuitous process.*

Oleaginous and other Globules.—One of us has already published an account of these bodies, which form a striking feature in the yolk of many Teleostean ova (No. 125). The following remarks refer mainly to *T. gurnardus*, and they still further explain certain statements in the paper referred to.

In the ripe ovum of the gurnard the globule (Pl. V. fig. 5, *og*) is of a dull pinkish hue under a lens, while by transmitted light it exhibits a brownish yellow or pale salmon-tint. It is enveloped by a protoplasmic pellicle which sometimes appears incomplete, and forms an equatorial line, with pale pinkish vesicles studded along its border. Unlike those forms in which the globule is imbedded in a definite pocket (*e.g.*, *Motella*), the globule in the gurnard, as also in *Cyclopterus* and *Cottus* (Pl. I. figs. 2, 3), is most mobile, and can be made to pass under the disc when the latter is uppermost. On rolling the egg the globule emerges from beneath the disc, and is liberated with a bound at the edge of the rim. Moreover, in passing round it flattens out, and again contracts its diameter, or rather resumes its more spherical form. At times the globule appears to ascend directly through the yolk, though this may be a deceptive appearance, for Ransom found in the very mobile globules of *Gastrosteus*, that while they passed freely through the yolk, they could not be made to go "through its centre to get to the uppermost segments when the egg is rolled round; in doing so the drops often separate to unite again" (No. 127, p. 436). Ransom accounted for this by the greater density of the central yolk-substance. The passage of the globule under the rim is well seen in the egg of the gurnard when the germ has extended as far as the equator. In certain morbid conditions the exact relations of the globule during its movements can be readily determined. Thus the globule is often firmly fixed in the dead egg between the opaque blastoderm and the yolk, or the globule is seen at the side, and cannot be made to pass beneath the disc, possibly on account of the doubling of the edge of the disc, or because the investment of the globule and the periblast have become dense and rigid. During the earlier morbid stages, however, the globule is observed to pass beneath the somewhat opaque disc, and in certain abnormal cases, from pathological change, the globule rolls external to the disc.

From the above observations it is evident that Mr Cunningham's view (No. 48, p. 6; also Pl. II. fig. 19) that the globule moves in the perivitelline space—that is, between the yolk and the zona radiata—is not borne out, since in experiments, such as the above, it passes between the disc and the yolk, and never passes through the protoplasmic cortex of the latter, save in rare morbid examples. In those eggs in which the rim has still a short distance to traverse the globule continues freely movable, and its surface next the yolk often presents a series of small globules and a single large central one. The

* *Vide* "Significance of the Yolk in the Eggs of Osseous Fishes," E. E. Prince, *Ann. Nat. Hist.*, July 1887.

globule passes in later stages under the embryo, and for some time moves freely; but about the fifth day, when the blastopore closes, it becomes fixed, generally at the point coinciding with the vegetal pole. It now exhibits a thick layer of protoplasm, which becomes vacuolated in a complex manner, and gives origin to numerous nuclear structures as well as pigment-spots (Pl. XI. figs. 12, 13). In certain cases (gurnard) the periblast was observed to bend in from the blastodermic layers, and carry the oil-globule with it at its margin.*

Perivitelline Space.

This space is generally very distinct, and contains a transparent fluid, usually said to be water, which enters the ovum after fertilisation. In an undetermined species the space is enormously enlarged (Pl. XIII. fig. 3). Reichert, however, very lately observed that under the action of nitric acid it exhibited whitish flakes (No. 134, p. 463). Ransom again states that when the funnel of the micropyle is withdrawn from the *discus proligerus* (in *Gastrosteus*), water enters "to fill the breathing chamber." This view was questioned by one of us in a short paper read at the British Association in 1885 (No. 122), the following statement being made:—"That a certain amount of water finds access to this space is possible, but in stained sections the fluid filling the chamber often appears coagulated and faintly stained, thus indicating the presence of minute protoplasmic particles. It would appear to be, therefore, a dilute plasma." Raffaele has recently stated that the fluid is albuminous (No. 125*a*). In the gurnard various granular bodies, probably portions of protoplasm of a circular form, have been seen. It is possible that these agree with the segmenting corpuscles of Ryder and the expulsive bodies of Raffaele.†

III. Extrusion and Deposition.

The ova when ripe either pass directly into the body-cavity from the ovaries and out by an external pore, as in the Salmonidæ and *Anguilla*, or they pass to the posterior end of the ovary as they become mature, and thence by an oviducal aperture to the exterior. The latter is the more prevalent mode, and it presents two types according as the act of deposition is very rapid, as in the Cottoids, Discoboli, and certain Blennies; or it is slower, as in the Gadidæ, and may be even prolonged, as appears to be the case with *Trigla*.

The difficulty of ascertaining the real facts in regard to oviposition is apparent when it is remembered that, about even so familiar a form as the salmon, opinion has been up till comparatively recent times divided; the fishermen being of opinion that the process is gradual, and may occupy many days, whereas there is much evidence to show that the ova are discharged all at once, or very rapidly. In stripping a ripe female the

* J. A. Ryder (*Amer. Nat.*, vol. xx. p. 987) states that the periblast is hypoblastic, and that the only source of the nuclei in the pigment-cells of the oil-drop must be periblast; therefore these cells are hypoblastic in origin. Kingsley and Conn severally observe (*op. cit.*, p. 188) that possibly the ova of all the Gadidæ have one or more conspicuous oil-globules in the deutoplasm.

† *Op cit.*, p. 16. He also thinks the perivitelline space has a phylogenetic significance.

eggs run out with little or no pressure, and the ovaries may often be thus emptied in a few moments. Now if the ovaries of a female *Cyclopterus lumpus*, exemplifying rapid deposition, be examined, we find, when in a ripe condition, that the contained ova apparently become mature simultaneously.* In such a case great distension of the abdomen occurs, and the eggs are deposited in a single large mass in a very short time. In a female *Cottus scorpius* under observation, and likewise distended with ripe ova, oviposition occupied only a few seconds.

A very different condition obtains in other forms, such as *Molva vulgaris* or *Pleuronectes flesus*, in which a large proportion of the ova ripen together, yet the act of extrusion is more deliberate and slow; while in *Gadus morrhua*, or more distinctly in *Trigla gurnardus*, the eggs reach maturity by successive strata, a comparatively small proportion of them being ripe and translucent. The latter generally pass posteriorly, and collect near the genital opening—ready for extrusion.† Isolated ripe ova, however, are scattered throughout the ovaries, and in such forms the extrusion of all the eggs in a single female must extend over a prolonged period.

While the ova remain in the body of the fish they are bathed in a mucilaginous fluid, so that they easily glide over each other, and thus their egress is facilitated. This ovarian mucus seems to have different properties in different species of Teleosteans, either disappearing on mixing with water, as we see especially in the non-adhesive floating eggs of the cod, haddock, whiting, ling, gurnard, skulpin, flat-fishes, and also in the demersal eggs of the Salmonidæ, or remaining glutinous and adhesive for some hours—the eggs clinging strongly together and forming irregular spongy masses, as in British Cottoids, Discoboli, various species of *Gastrosteus*, as well as the recently discovered ova of *Anarrhichas*. In *Lepadogaster*,‡ however, the ova are fixed singly to shells, sticks, sea-weeds, and other structures.

After submergence in sea water such ova become so strongly cemented that some force is required to separate them, and the egg-masses of forms like *Cyclopterus* adhere so firmly that many of the ova are usually injured in dislodging them. Whether the mucilaginous nexus which binds ova like those of *Lophius piscatorius* together in considerable masses, or forms a thick, tenacious layer outside the zona radiata in eggs such as those of *Perca fluviatilis*, be really an excessive secretion of the mucus spoken of above or not is undetermined.

Demersal ova appear to be deposited by the female on the very sites where the whole course of development, up to the time of hatching, will be undergone. With pelagic ova the case is very different; during development they may wander far from the place of deposition.

It must be noted, however, in the case of the cod, and other food-fishes, that the grounds upon which the adults congregate are those where the surface specially abounds with their pelagic ova, as Sars first noted at Lofoten.

Upon extrusion the buoyancy of pelagic ova is strikingly shown, for, if ripe, they at

* *Vide Nature*, June 1886. † *Vide* No. 104, p. 363, &c. ‡ *Vide* No. 106, p. 434.

once ascend like minute crystalline globes of oil, and before fertilisation, as well as after, they swim freely in the water (No. 11, p. 36, and No. 65, p. 450). Not only are these pelagic ova found at and near the surface of the sea, but, in many areas, throughout the greater part of its depth. Moreover, they occur in great numbers near the bottom. In calm regions they congregate near the surface in scattered groups, and show no tendency to adhere together, save in such exceptional instances as those before mentioned. The slightest agitation scatters them, and they are carried to and fro by the currents in the surrounding medium.* In very still water in tanks they often form layers extending over a considerable area, the lower strata sustaining by their buoyancy the superimposed layers, which are even and regular to a remarkable degree (Pl. I. fig. 10). Their buoyancy is readily affected by a variety of conditions, especially by adulteration of the sea water in which they float. In impure sea water† and in fresh water they sink, as they also do in alcohol, in which fluid they rapidly become opaque. Dead eggs never float, and dying eggs, though remaining translucent, lose their buoyancy. Healthy eggs are rapidly affected by unhealthy or putrid ova in their vicinity, a fact showing that the zona radiata is pervious, and that endosmosis and exosmosis readily take place, as indeed the absorption of water by the partially desiccated ova of the cod (*vide* p. 681) clearly shows.

In demersal and pelagic ova unhealthy or dying eggs are readily recognised by the opacity of their contents; and an offensive odour, if the eggs are in masses, indicates that they are dead. Small groups of demersal ova, such as those of *Cottus* and *Cyclopterus*, when dead, may be kept for many weeks in still water in a flat vessel without undergoing much change in outline, though of course opacity is complete.

Fertilisation.—With very few exceptions (*e.g.*, *Gambusia patruelis*,‡ *Sebastes norvegicus*, and *Zoarces viviparus*) the ova of Teleosteans are fertilised after expulsion by the shedding of the milt, on the part of the male, in their neighbourhood. The rapid diffusion of the milt in water by the serpentine movements of the spermatozoa is very striking—they spread through a large area, and in tanks used for artificial fertilisation and rearing it is difficult to keep ova in an unfertilised condition if sperms can by any possibility find access through the supply-tank.§

In demersal ova deposited on the sea-bottom, on zoophytes or shells, or (in littoral forms) beneath shelving rocks, in hidden nooks of tidal pools, and in some cases in nests constructed by the male fish, fertilisation is usually ensured by the proximity of the male, which may even carefully guard the ova during development, as is notably the case in *Cyclopterus lumpus* (*vide* No. 107, pp. 81, 82); but even in this species masses of eggs occasionally are found whose fertilisation has not been accomplished. This may sometimes happen in the case of pelagic ova, though experiments at the Laboratory have shown that eggs of haddock may remain for a considerable time unfertilised, and yet be

* See Hensen's observations proving that pelagic ova are widely scattered in the sea (No. 65, p. 449).

† *Vide* No. 104. ‡ No. 141, p. 461.

§ As occurred to Professor Ewart and Mr Brook at the Rothesay Aquarium, and also with *Motella* in the St Andrews Laboratory.

successfully fecundated—a series of ova of the species named being fertilised sixteen hours after oviposition; and in the case of the ova of the herring from the deck of a fishing boat, G. Brook states that forty-eight hours have been allowed to elapse, yet fertilisation was found to be successful.

More uncertainty probably exists in the case of pelagic ova, which after expulsion are never quiescent, but may travel over large areas, so that at times their fertilisation must be a matter of chance. The fishes at the spawning season congregate, it is true, in vast numbers, males and females thus herding together; but ripe females may occasionally shed their ova where it is problematical whether sperms will ever reach them, and in this way we can account for the quantity of dead eggs of plaice and cod which Hensen found while dredging in the inner bay of Kiel (No. 65, p. 429), though changes in the nature of the water have also to be taken into account. If no spermatozoa reach them within a limited time after extrusion, pelagic eggs lose their glassy transparency, and descending to the bottom assume the white opacity and wrinkled appearance of dead ova. In demersal forms, with a denser capsule, the unhealthy or dying condition is not so readily seen; but opacity of the contents, and especially an increasingly offensive odour, if in masses, are unmistakable indications of loss of vitality.*

The relation of the micropyle to effective fertilisation has been already treated of; and many authors regard its position as of the highest importance. Gerbe, indeed, satisfied himself in the case of the trout that this position is always superior, and he took pains to secure this condition when performing artificial fertilisation (No. 57, p. 330). In the uppermost segment he found after fertilisation that a granular layer is formed by a process of thickening, so that a "nuage vague" condenses as a circular area always in relation to the micropyle. Gerbe would extend the observations he noted in the trout to the ova of Teleosteans in general, and certainly in many demersal forms the blastodisc concentrates in the uppermost segment, and the micropyle is stated to be uppermost; yet in pelagic eggs the disc would appear always to be formed at the inferior pole, and in such eggs if the constancy of the position of the micropyle be well founded, it must be no longer uppermost, but on the under side of the egg, and such is affirmed to be the case, though there are difficulties in the way of such an affirmation, and many reasons for holding that the position is not necessarily constant.

Demersal ova do not show a uniformity in the situation of the micropyle, for in the egg-tubes of *Perca* it is not uppermost, but directed to one side, so that it opens into the lumen of the cylinder; and Gerbe found that it occupies a like position after fertilisation in *Salmo fario*, the capsule he says, moving through a quadrant, so that the micropyle is no longer uppermost; "this change simply alters the respective positions of the cicatricula and the micropyle, and when accomplished the phenomenon to all intents and purposes is ended" (No. 57, p. 331).

* The ova of *Osmerus eperlanus* would seem to become opaque very rapidly, for Cunningham notes that the unfertilised eggs sank to the bottom, remained unattached and free, and became opaque-white shortly after expulsion, though at first they were of a translucent yellow (No. 49, p. 293).

The artificial fertilisation of the eggs of osseous fishes is easily performed, it being only necessary to apply ripe spermatozoa (Pl. I. fig. 9) from the male to mature ova placed in water. If ova and the male element be placed in the same vessel of water, the process is accomplished in a few moments. The exact mode by which it was really accomplished remained unknown until Ransom not only saw and truly interpreted the micropylar opening, but watched spermatozoa make their way into the aperture.* "I saw," he says (No. 127, p. 461), "an active spermatozooid enter the apex of the funnel, and disappear as if inwards; a quarter of a minute more had not elapsed before the bright circle which marks the aperture became indistinct from shortening of the funnel; during the next two minutes I saw three more spermatozooids enter the apex and vanish apparently inwards." Notwithstanding the clear and unmistakable observations published by Ransom, the process of fertilisation is one about which much discussion has taken place. Kupffer, as already mentioned, has even doubted that the micropyle plays any essential part in fertilisation (No. 87, p. 179); and Boeck has advanced a theory of endosmosis which is somewhat like the explanation Newport put forward in one of his earlier treatises, when, having failed to detect in the ovum of *Rana* any perforation or fissure by which sperms could find access to the egg-contents, he said that mere contact with the external envelope must suffice for fertilisation, as he never found spermatozoa in contact with the yelk-membrane, or even within the substance of the external envelope (No. 112, p. 203). This endosmotic theory Newport afterwards abandoned, and adopted the opinion which Dr Martin Barry had put forward—in accordance with the views of Leeuwenhoek, and Prevost and Dumas (No. 121), that the spermatozoa penetrate bodily into the ovum (No. 21, p. 309). Ransom's explicit account decides the matter, the situation and structure of the micropyle clearly indicating its purpose, viz., the admission of the spermatozoa to the germinal elements within the ovum (No. 127, p. 462). G. Brook, again, has recently affirmed that in *Clupea* spermatozoa enter on all sides. The interesting question remains as to whether one or more spermatic bodies are concerned in the normal fecundation of a single ovum. The presumption that one spermatozoon suffices is strong, but there are peculiar difficulties in the case of the Teleostean ovum in actually observing the fact. The entrance of these bodies has been watched in many Invertebrates, and one spermatozoon is usually found competent to effect fertilisation, though Selenka found (in *Toxopneustes variegatus*) that while one usually enters, several may find access, and normal development still follow. Three or four indeed sometimes enter, as Hertwig and Fol observed in the same species, and the separate pronuclei formed by each usually fuse with the single female pronucleus; but they found that subsequent cleavage was irregular (No. 66). In *Petromyzon* Calberla's investigations show that one sperm only enters, the enlarged head-portion separating at the outer micropyle from the tail which is left behind, while the head penetrates the yolk or rather passes along a protoplasmic process, which penetrates the yolk and reaches the female pronucleus at the inner extremity (No. 38, p. 464). Kupffer and Benecke, again, found that several sperms

* Doyère had previously seen the micropyle in *Syngnathus*.

may enter in this form (No. 89). In osseous fishes a similar condition would appear to obtain, one spermatozoon being sufficient; but as this does not plug up the micropyle, others may also enter, indeed, RANSOM observed this in *Gastrosteus*. "I watched closely one egg," he says, "which was placed with the micropyle in full face, so that the aperture at its apex was well seen. Spermatozoa approached and entered the funnel, and one was watched till it disappeared, apparently in the direction of the interior of the egg, just at the moment when it seemed to occupy the aperture at the apex of the micropyle. Immediately after the depth of the funnel began to diminish, and a breathing chamber commenced to form; two or three more spermatozoa were, less distinctly, seen playing about in the apex of the funnel as it was shortening; one of them appeared to become still before it vanished apparently inwards" (No. 127, p. 461). The exaggerated length of the micropylar funnel, which RANSOM describes in *Gastrosteus* as enabling it to dip into the granular discus proligerus, has not been described in other Teleosteans. Neither ANDRÉ nor GERBE mention it in the trout, nor does HIS show it in the trout or salmon; while in pelagic eggs the micropylar eminence, though distinct, is not by any means prominent (Pl. I. figs. 11–14). A lengthened micropyle is indeed unnecessary, the mere presence of the spermatozoon within the ovum being the essential point. The actual entrance of sperms has been seen in very few Teleosteans. RANSOM, as already noted, saw them occupying the external orifice of the micropyle, and ANDRÉ speaks of observing a sperm apparently entangled, in the micropylar canal, by the jutting ends of the radial striæ, which appeared to him to serve for securing the sperm after its entrance (No. 4, p. 201); but there seems to be no column of protoplasm facilitating the passage of the sperm from the micropyle to the female pronucleus, such as CALBERLA describes in *Petromyzon planeri*. The head of the sperm in this form separates from its flagellum, and passes along the protoplasmic column, which withdraws from the micropyle (CALBERLA'S äussere Mikropyle), and the sperm proceeds through the neck of the column (distinguished as the inner micropyle) to the enlarged central termination, where the "eikern" or female pronucleus is seated. Here conjugation of the two pronuclei is effected (No. 38, p. 458, Taf. xvii. figs. 5, 6, 7, and 8). Possibly the preformed discus proligerus may represent this column; and in those Teleosteans in which no disc is formed, the distance between the inner orifice of the micropyle and the protoplasmic cortex of the vitellus is insignificant. The spermatozoa of Teleosteans seem to be of the ordinary type, and show, so far as observations go, little difference in structure—the usual head or enlarged portion being distinguishable from the hair-like tail or flagellum (Pl. I. fig. 9).

Polar Globules.—The details of the phenomena of fertilisation in osseous fishes are probably not unlike those in forms more fully known. HOFFMAN has described the formation of the pronucleus and ejection of a polar globule in *Scorpæna*, *Julis*, and *Crenilabrus*, and he states that the globule closes up the orifice of the micropyle, and prevents the admission of other sperms after that of the single sperm which

accomplishes fertilisation.* He, however, states that the extrusion of polar bodies, the disappearance of the nuclear spindle, and the aggregation of the germinal area may take place independently of impregnation. KINGSLEY and CONN† describe and figure a polar globule in the egg of the cunner apparently after maturation. The globule appeared in the centre of the aster, and passed through the micropyle. LIST recently does the same in *Crenilabrus pavo*, the body being globular at seven minutes and rod-like at thirty minutes.‡ RYDER noted in the ovum of *Gadus morrhua* a minute granular papilla projecting from the early germ, and looked upon this as representing the polar cells derived from the germinal vesicle (No. 141, p. 477). In *Trigla gurnardus*, twenty-five minutes after the addition of sperms, a somewhat cylindrical nuclear body has been observed in the superficial protoplasm (Pl. I. fig. 17, *a*). It exhibited very slow amœboid movements, and five minutes after it was first noted it had shortened and contracted in the mid-portion as if dividing into two—a wide granular border extending round it (Pl. I. fig. 17, *b*). Three minutes later the two separating parts closely approached, and the body became still more contracted and compact—the granular margin also becoming less (Pl. I. fig. 17, *c*); but the median cincture was still plainly marked ten minutes later (Pl. I. fig. 17, *d*). A side view of a similar structure in another ovum exhibited two spherical nuclear bodies enveloped in a vase-shaped mass of protoplasm, and from the centre of its wide upper surface radial striations diverged (Pl. I. fig. 17, *e*). No similar appearance has been observed in other pelagic ova seen by us. Mr CUNNINGHAM was more fortunate with the ovum of *Pleuronectes cynoglossus*, and he describes a polar globule in this species.§

The more obvious features in the living ovum after fertilisation are—(1) The meridional streaming of the cortical protoplasm to the animal pole. (2) The formation, or, in certain forms, the visible increase in the size of the blastodisc, and its assumption of a more definite contour. (3) The disappearance of the minute clear vesicles which stud the entire cortex of the vitellus, probably as a consequence of the transference of the protoplasm to one pole—by which they are carried to the region of the disc. In many forms a change in the optical appearance of the yolk is seen. RANSOM noticed this, and says that the increased clearness and translucency of the yolk is in part due to distention and greater transparency of the enveloping layer (No. 127, p. 458); indeed, the whole ovum after fertilisation assumes a brighter and more tense appearance. Finally (4), a space slowly becomes apparent between the vitelline globe and the inner surface of the zona radiata, so that the egg-contents are no longer closely applied to the capsule, as in the unfertilised ovum.

Probably the foregoing features mark the fertilised condition in all Teleostean ova; but there are many forms in which, for various reasons, they cannot readily be discerned.

* This closure of the micropyle is perhaps incomplete, as the subsequent formation of a perivitelline space is due to the entrance of water in the main through the micropyle, though it may also enter by the general surface.

† *Loc. cit.*, footnote, p. 190.

‡ *Op. cit.*, p. 597, fig. ii. *d*.

§ *Op. cit.*, p. 131.

Especially is this the case in ova which show a preformed discus proligerus. In the pike, for instance, LEREBOULLET states that both are alike, save in the formation of a "disque huileux" which collects in the fertilised egg, as GERBE also describes in the egg of the trout, two hours after fertilisation, the circular germinal area appearing as if enclosed in a "crown of oil-globules" (No. 57, p. 330); yet even this feature may appear in the unimpregnated egg, and it cannot therefore, as LEREBOULLET confesses, be traced to the action of the sperm (*vide* No. 93, p. 478). The fertilised ovum in pelagic forms (*e.g.*, cod and gurnard) is more readily distinguished, as the segregation of the protoplasm is plainly visible within an hour or two after fertilisation; but the transference is not to the upper pole, as in a large number of demersal forms, but to the lower pole, where the patera or flattened disc is formed of clear, straw-tinted protoplasm containing minute spherules, which are especially numerous at the base and periphery. During the process of segregation the contour of the vitellus becomes very distinctly corrugated—an appearance produced by the streaming of the protoplasm along definite meridional lines; and pelagic forms are especially favourable for observing this polar transference. RANSOM, in common with other observers, wholly failed to detect this movement (No. 127, p. 458), though he says that the granules often form radial lines round the margin of the concentrating disc (*Ibid.*, p. 459). Besides passing along the superficial areas, much protoplasm probably also glides in the deeper strata of the vitellus to the base of the germ during the first hour after entrance of the sperm. Such streaming of the protoplasm towards the disc has been noted by many observers, and recently KOWALEWSKY has described it in *Carassius*, *Polyacanthus*, and *Gobius* (No. 86). In two hours or more, according to the temperature and other conditions, a plano-convex disc is formed, composed of an almost homogeneous matrix. The disc in the fertilised ovum is always well defined and prominent, and continues to receive additions of protoplasm, so that it increases in size, and becomes more pronounced; whereas in the unfertilised ovum, when a disc is formed, it becomes "vague, irregular in outline, and loses coherency" (No. 57, p. 330). The primary segmentation-nucleus has rarely been detected in the blastodisc before cleavage, granules and colourless vesicles alone appearing in its matrix. The breathing chamber gradually becomes more distinct; but this may also happen in the unfertilised condition, as RANSOM found that such ova may, after being in contact with water for an hour, show this marked interspace. Its formation, as well as the concentration of the disc, RANSOM holds to be only indirectly due to the spermatozoa, which may render more easy and rapid the influx of the surrounding medium into the egg (No. 127, p. 463). The same observer carefully studied the formation of this space in *Gastrosteus*, and states that it first appears close to the micropyle, whence it "gradually extends over the rest of the yolk-ball, being complete in three to five minutes after the spermatozooids have been applied" (*Ibid.*, p. 457); but in a note at the foot of the page he says that water may enter more freely, and the chamber arise simultaneously in the ova of other fishes. NEWPORT, who was the first to signalise this perivitelline space, speaks of it as "respiratory," and being in *Rana* "at first but a small area" (No. 112, p. 187), a view coinciding with RANSOM'S upon the same ovum, for

he believed he saw it arise, just as in *Gastrosteus*, near the micropyle. Most recent observers, including List, describe this perivitelline space in Teleostean eggs. To what is the formation of this chamber due? Does the vitellus, which before fecundation fills up the intra-capsular area, diminish, or does the external capsule really enlarge? On the one hand, Ransom maintains that the yolk-sac or capsule enlarges (No. 127, p. 457); while, on the other hand, Gerbe believes that, by the contraction of the vitellus, this "zone of separation" is produced (No. 57, p. 330). Keber has further surmised that part of the contents of the egg may flow out through the micropyle (No. 77), and the egg-mass would thus decrease. Kupffer considers that both the first mentioned phenomena happen, for he says that in *Clupea* not only does the yolk contract, but the capsule enlarges by as much as one-quarter of its diameter (No. 87, p. 185). A still more marked increase in size Lereboullet noted in the egg of *Perca*, which, he says, by absorption of water through the radial tubes acquires a volume twice that which it had before extrusion (No. 93, p. 471). Usually, however, the enlargement of the Teleostean ovum is so small as not to be readily noticed.

Movements of the Yolk.—The curious movements of the vitelline mass, which have been described by many observers, and are stated by Ransom to be "the most striking phenomena which follow on the entrance of the spermatozooids into the egg" (No. 127, p. 463), are not visible in all Teleostean ova. At any rate, if performed at all, they are obscure, or so imperceptible as to have escaped notice in pelagic ova, while in demersal ova they are occasionally not exhibited—Lereboullet indeed affirming that in *Perca fluviatilis* the egg-contents remain unmoved, and at no time show the intra-capsular movements so remarkably distinct in *Esox* (No. 93, p. 503). He further says—"I have not seen it (the rotatory movement) in the white fishes, of which I have observed many species, and M. Vogt has not noticed it in Coregonus." In addition to the undulations, or "oscillations" as Ransom terms them, which usually pass like a wave of contraction from one pole * to the opposite pole, and occasionally along the equatorial line, producing a dumb-bell outline in the latter case, there are rotations of the vitellus *en masse*. Ransom did not observe any rotation in *Gastrosteus*, which exhibits the oscillations very distinctly, nor did he in other ova, though he admits that such movements on the polar axis were not improbable. Lereboullet again speaks of another movement, in fact, a simultaneous double movement: the vitellus, he says, "exerce un mouvement de rotation sur son axe et un mouvement de translation autour de la coque" (No. 93, p. 497). These motions seem to continue during the early progress of cleavage, but cease, according to Lereboullet, when three-quarters of the yolk-surface are enveloped. He describes at this later stage, in *Esox*, an alteration in the form of the vitellus; it elongates and becomes pear-shaped, the narrowest diameter circumscribing the part of the yolk not yet covered by the extending blastoderm. Bambeke, in *Leuciscus* (?), described the same change of shape, and speaks of the opening (the blastopore, or *trou vitellaire* of C. Vogt) as resembling the mouth of

* Ransom says the pole at which the movements commence is that resting on, *i.e.*, in contact with, the capsule; but this can hardly be so.

a balloon (No. 20*a*). The change of outline Bambeke attributes to epiboly, the blastoderm squeezing the fluid yolk out of shape; and this is not improbable, for in various pelagic ova the naked yolk, *i.e.*, that part not yet covered, projects boldly from the blastopore like a plug pressed out from the diminishing aperture. The change in shape might be attributed to the contractility of the yolk—an inherent property according to Reichert (No. 134); but there is much reason for holding that the active agent is the amœboid protoplasmic cortex, or the blastoderm itself external to that layer. A most remarkable phenomenon was observed by Lereboullet in the ovum of *Esox* at the stage just referred to, when the usual rotation is perceptibly diminishing, for he states that the blastoderm seemed to continue its rotation "as if disconnected from the yolk, and the latter continued to turn from right to left as though inside a loose sac" (No. 93, p. 491).

What the significance of these varied movements really is cannot be definitely stated; but that they are connected with the separation of the germinal matter from the food-yolk proper, as Ransom surmises, seems very probable. Ransom, indeed, would go further, and regard them as a form of contractile movement, not remotely connected with segmentation (No. 127, p. 495); and it is noteworthy that these movements cease when the germinal matter has, for the most part, separated from the trophic element in the vitellus. The yolk alters its form soon after fertilisation, as Lereboullet observed in the pike; and he refers to a movement of the constituent elements of the egg—the marked flattening of the spherical yolk, which now becomes elliptical (see No. 127, pl. i. fig. 17), while the blastodisc projects prominently from its surface.

Whether the yolk-matter itself, or the protoplasmic envelope outside, really produces the rhythmic contractions referred to, the phenomena depend, as Ransom found, upon the presence of oxygen in the surrounding medium, while carbonic acid produces total cessation or a marked repression of these movements (No. 128, p. 237). They seem to demand less oxygen than cleavage proper (No. 127, p. 495), though the amount of oxygen used is small; and Ransom did not succeed in obtaining chemical evidence as to the products of the oxidation which undoubtedly goes on.

The conclusion that all the movements collectively known as yolk-contractions are connected with the polar segregation of the germinal protoplasm, is probably near the truth. That their existence, or at any rate their vividness, is correlated to peculiarities in the early development of the germ there is no proof, and Ransom's conclusion is very much at variance, indeed, wholly opposed to the facts, when he says that such movements in *Esox* and *Gastrosteus* are connected with rapidity of development (No. 127, p. 495). These forms, instead of hatching in a shorter time than those with slow or indistinct contractions, have an embryonic development unusually prolonged, so that the reverse of the above conclusion is really true, viz., that the ova in which these movements are not merely indistinct but imperceptible, are of all forms the most rapid in development, and of such rapidly developing eggs those of the Gadidæ and Pleuronectidæ are marked types.

IV. Segmentation.

At the time segmentation begins (always within a few hours after fertilisation) the process of segregation is to a great extent completed, and the germinal disc is defined as a thickened patera of clear protoplasm lying upon the yolk in those forms whose upper segment is the animal pole, or depending from the yolk in those ova with an inferior animal pole, and separated by an intermediate stratum, which differs both from the yolk and the germinal matrix. Thus ova of the haddock, fertilised at 2 P.M. on 23rd March 1886, showed at 8.50 P.M. a uniform prominent mass or cap of protoplasm without trace of segmentation. At the margin were numerous protoplasmic processes, rising in some cases on the surface of the yolk into globules. On the second day the rim of some of the granular spheres projected beyond the disc at the lower pole. Whether the separate cells, seen during development, in the perivitelline space are due to these projections is unknown. In the cod, again (see Pl. X. fig. 9), the spheres, which differ in size, show minute granules. The nuclei of the spheres are not always easily seen in the living egg, but with due care can generally be made out.

Ryder is right in saying that the cleavage does not at first go quite through the disc, the contrary being stated by Kingsley and Conn. The latter authors noticed marked amœboid movements at the 4- and 8-celled stages, processes being sent out by the spheres.

In the early stage of segmentation the Teleostean egg shows external larger spheres and internal smaller ones (Pl. IX. fig. 8), just as Janosīk* found in *Crenilabrus* and *Tinca*, the internal dividing more quickly than the external. This, likewise, is observed in the Elasmobranch egg.

We have seen that all the features of the fertilised ovum may appear to some extent in the unfecundated egg, and though segmentation is usually an indication that fertilisation has taken place, it is not infallibly so. Oellacher found cleavage-lines passing across the germ in an unimpregnated egg of the fowl (No. 113),† and in Teleostean ova the disc may break up into segments by an irregular kind of cleavage. Its abnormal character is soon revealed, resembling as it does the cleavage of unhealthy and dying eggs, the cells always showing great irregularity, and the protoplasm composing them assuming a more or less marked opacity or a granular appearance. Both in size and shape Lereboullet found that these abnormal cleavage-segments differed from the normal (No. 93, p. 485).

The Cortical Protoplasm.—The blastodisc is formed by the segregation at one pole of protoplasm, which, moreover, constitutes a superficial and tenacious layer around the vitellus. This layer is itself derived by centrifugal transference from the scattered protoplasm mingled with the general matrix of the yolk, a phenomenon which recalls the formation of the periblastula in the crustacean ovum, such as that of *Astacus*. In this ovum

* *Archiv f. Mikr. Anat.*, vol. xxiv.

† Bischoff (*Ann. d. Sci. Nat.*, iii. sér., Zool., t. ii.), Hensen (*Centralblatt f. die Med. Wiss.*, 1869), Kidd (*Quart. Jour. Micr. Sci.*, xvii., 1877), and others have confirmed Oellacher's observation in other forms, especially Mammals.

the protoplasm interfused with the yolk also collects at the surface, though it is not visibly separated by a line of demarcation, and can only be recognised by its texture and property of readily staining. Ere long it completely separates from the granular deutoplasm, and forms a superficial blastodermic layer enveloping the yolk.* In the same manner a protoplasmic cortex, like the periblastula just mentioned, forms an equal layer over the yolk in fishes' eggs, but is not at first sharply defined, though later it is so. Balfour observes that in Elasmobranchs the disc is merely a part of the ovum in which the protoplasm is more concentrated, and the yolk-spherules smaller than elsewhere.

In the ova of the haddock on the second day the blastodisc shows small "oil-globules" amongst the protoplasm between the spheres, and the disc presents a pale salmon-tint by transmitted light. Usually it appears to consist of homogeneous protoplasm, with numerous small spheres of oil or indifferent fluid and scattered granules. In *Clupea harengus* no cortical layer is present before segmentation, according to Kupffer (No. 87, p. 179), nor is a blastodisc preformed, this latter feature being shown also by Gadoid and other pelagic ova, though in these eggs a cortical layer is well defined before fertilisation. Notwithstanding that the cortex seems thus sharply marked off from the yolk, there is good reason to believe that the centrifugal movement of the deeper interfused protoplasm does not cease when the layer is formed, and Klein refers to this process as the feeding of the cortex upon the yolk for purposes of growth (No. 79). Balfour also speaks of certain nutritive elements of the yolk as being converted into protoplasm (No. 11, note at foot of p. 679), and Kupffer (No. 88, p. 214) and Rieneck (No. 137) have adopted a similar view, as also more recently has G. Brook (No. 30).

No nuclei can be detected in the cortex; but clear structureless spheres occur in small groups, or singly over its surface, and these coalesce later, and form larger spheres, which are found at the base of the blastodisc during segmentation. Ryder has determined their composition to be that merely of an indifferent fluid (No. 141, p. 467). Outside this cortical protoplasm Ransom distinguishes a delicate homogeneous layer, his "inner yolk sac," which is not possessed by the more immature eggs. In "the smallest intra-ovarian ova" examined in saliva, he says "the yolk is granular and irregular, not smoothly defined as it would be were an inner sac present" (No. 127, p. 442); and in ova two-thirds their full size, also, he failed to perceive it. When intact it seems able to resist osmotic currents in *Salmo salar*, and it varies in bulk, being unusually thick in the ruffe (*Acerina*) (*Ibid.*, p. 453).

Such an inner-sac would appear to be absent in Gadoid and similar pelagic ova, and indeed in the forms studied by Ransom the precise nature of the so-called inner-sac is a subject for further investigation. He regards it as a membrane, as performing contractile movements, and as folded in along the lines of blastodermic cleavage (No. 127, p. 479).

It is difficult, however, to conceive a structure, meriting the name membrane, enveloping yolk and germinal disc so closely as to be almost inseparable, and involved in the

* *Vide* Reichenbach, "Die Embryonalanlage und erste Entwickelung des Flusskrebses," *Zeit. f. w. Z.*, xxix., 1877.

cleavage-process. The view that it is simply the cortical protoplasm, and not a definite membrane (*vide* No. 122, p. 445), is supported by certain facts which RANSOM mentions, for he speaks of the inner face of the yolk-sac as ill-defined and closely connected with the formative yolk (No. 127, p. 433), and that on rupture the shreds change their form (*Ibid.*, p. 478) and are frequently drawn out into thread-like prolongations (p. 468); while he further describes it as continuous with the blastoderm (p. 467), and admits that, as it ultimately shares in the cleavage process, it "may to that extent be considered a part of the formative yolk" (p. 433) or germinal protoplasm. The presence of a like membrane investing the germ has been maintained by SCHENK in the ovum of Elasmobranchs (No. 142), but other observers, including LEYDIG and BALFOUR, have denied its existence. The yolk-sac described in the hardly mature ovum of *Rana* by CRAMER (No. 45, p. 33) as a distinct membrane before cleavage begins, is merely the more consistent superficies of the yolk-ball, and not a separable structure. The fact seems to be that what RANSOM regards as a distinct membrane is the cuticular stratum of the protoplasmic cortex, and is therefore less of the nature of a sac than that of an external layer, slightly more consistent than the protoplasm underneath. RANSOM admits that in a sense it may be so regarded (No. 127, p. 433); and it is adherent to the blastodisc, over the outer surface of which it passes, and probably constitutes the clear matrix, as distinct from the granules of the disc. It forms folds at the margin of the clefts during segmentation, "reminding one," he says, "of the 'Faltenkranz,'—described by REICHERT and by SCHULTZE in the frog's egg,"—these folds being in fact the familiar corrugations produced by the cleavage and separation of the blastomeres. Sections through the disc at this time show no investing membrane, though it is true that the cortex takes a slightly deeper stain than the underlying matrix of the blastomeres, but the one insensibly passes into the other. BALFOUR also found, in the ova of Elasmobranchs, that the surface was very susceptible to stains, and that the sides of the furrows took a deep colour; but such appearances did not suffice, in his view, to demonstrate a separate membrane, so that in Teleosteans, also, we must, with LEREBOULLET, affirm "l'absence de membrane propre" (No. 95, p. 13) outside the blastoderm. That RANSOM's layer is simply the cortical protoplasm is shown by the fact that on rupturing it no coherent layer beneath held in the contents, but the food-yolk immediately flowed out (No. 127, p. 465). RANSOM himself also speaks of the formative yolk as a layer investing the yolk-ball. We cannot, therefore, recognise an inner yolk-sac as such, for the somewhat viscid and coherent layer, which alone appears to envelop the yolk, would behave precisely as RANSOM's yolk-sac did, when in contact on its inner side with the semi-fluid yolk, and on its outer side with the watery perivitelline fluid. The whole of this cortical protoplasm, however, does not enter the blastodisc and undergo segmentation; a considerable part never reaches the animal pole, but permanently clothes the yolk-globe, and part of it may temporarily form a supplementary disc at the vegetal pole, as KUPFFER saw in *Clupea* (No. 87, p. 185); while a portion remains as a sub-blastodermic stratum, and becomes thickened as a peripheral wall, the nuclear zone,

or periblast proper, around the margin of the disc. A thin stratum may also be distinguished creeping over the segmenting blastoderm as an external pellicle, referred to before as probably homologous with RANSOM's inner sac, and this layer sends down processes which fill up the interspaces between the large primary blastomeres (Pl. II. fig. 1, *p*). This appearance, which is distinctly seen in sections of the early blastoderm, may, it is true, be really the dilute plasma, or perivitelline fluid, penetrating the inter-blastomeric fissures, though more probably it is periblastic protoplasm, forming an intermediary substance, such as LEREBOULLET distinctly recognised (No. 93, p. 493), and as E. VAN BENEDEN figures (No. 25, pl. iv. fig. 7, &c.).

To sum up briefly, we may say that the protoplasm interfused with the food-yolk continues from a late intra-ovarian stage to collect superficially as a cortical layer, and forms—

(1) The blastodisc at the animal pole, and in rare cases a transient pseudo-disc at the vegetal pole (Pl. II. fig. 1, *bdm*).

(2) The intermediary, or sub-blastodermic layer (Pl. II. fig. 1, p^1).

(3) The thickened marginal wall or periblast-ring (Pl. II. fig. 1, *per*).

(4) The superficial envelope and inter-blastomeric substance of the segmented disc (Pl. II. fig. 1, p^2).

(5) The sole intra-capsular envelope of the deutoplasmic globe or yolk, prior to the epibolic extension of the blastoderm (Pl. II. fig. 1, p^3).

The Subgerminal or Nutritive Disc.—Reference has been made to the layer of protoplasm beneath the blastoderm proper (Pl. II. figs. 1 and 15, *a*, *b*, *c*, *d*, *e*—*cp*), and it has been distinguished from the periblast proper, *i.e.*, the thickened peripheral wall, and the nuclear zone round the margin of the disc, by various names, such as "intermediary layer" (BAMBEKE), "disque huileux" (LEREBOULLET), "Rindenschicht" (HIS), "median lens or lentille" (E. VAN BENEDEN); while other observers, *e.g.*, HAECKEL and RANSOM, have not recognised it, the latter indeed saying of the blastodermic surface in contiguity to the yolk, that it seems to be merely "the corpuscles resulting from segmentation in contact with the fluid-yolk" (No. 127, p. 467). It appears to arise like the rest of the protoplasmic envelope of the yolk by superficial segregation, though BAMBEKE attributes its formation to a centripetal extension of the peripheral annulus; but LEREBOULLET's statement probably represents the origin of this sub-blastodermic stratum more truly, when he says that in *Esox* and *Perca* it arises simultaneously with the disc, these nutritive elements, as he calls them, following the plastic element in their migration to the animal pole (No. 93, p. 11), and at the earliest stages may, as KUPFFER supposes, give nutriment to the germinal disc (No. 87, p. 194). RANSOM did not distinguish a stratum, however, but speaks of "a collection of dark oil-granules distinct from the large drops which float in the yolk." He saw granules and globules of oil below the disc, and as these are consumed during the development of the germ-mass, it is probable that a kind of yolk-digestion goes on.

Lereboullet, Kupffer, Rieneck, and Oellacher all noticed the accumulation of globules under the disc in impregnated ova; and Bambeke (who quotes them) says these indicate food-particles for nourishing the germ. Gerbe figures a crown of oil-globules around the periphery of the disc (No. 57, p. 330, pl. xii. figs. 3 and 4, *b*); while Oellacher speaks of his lenticular germinal mass as including a lower layer which imprisons many oil-spheres, and at times is seen to be separated by a distinct contour from the disc. Oellacher regards it as part of the blastodisc, and Bambeke likens it to his intermediary layer, though the subgerminal disc has been distinguished as a separate structure, neither to be confounded with the lower part of the germinal disc nor with the intermediary layer. Lereboullet indeed distinctly affirms that his mucous layer underlies, as a definite membrane, the blastoderm, while it rests upon the nutritive disc. Bambeke erroneously likens his intermediary layer to this stratum beneath Lereboullet's mucous layer in the trout (No. 20*a*). In Lereboullet's view, three distinct strata must be recognised at the animal pole—(1) the germinal disc proper, (2) the mucous or intermediary layer, and (3) the "disque huileux" or nutritive layer. The separation of the stratum underneath the disc into two layers has caused some confusion, and the distinction is perhaps unnecessary. It is readily seen that the lower portion of the intermediary layer will be more fully charged with oily spherules and granules from the yolk than the portion in apposition to the base of the disc, but it is needless to separate it as a distinct oily stratum. A subgerminal stratum is probably not absent in any Teleostean ovum, though less prominently seen in some (*e.g.*, Gadoids and Pleuronectids) than in others (*Esox* and *Gastrosteus*), but the presence of a layer beneath the subgerminal stratum has been noted by very few observers. We cannot indeed regard Lereboullet's lowest (third) layer as separate from his mucous layer, which has been so generally recognised in Teleosteans. This single subgerminal layer, in whose lowest stratum oily spheres and granules are numerous, is the granular layer which Balfour speaks of, though in Elasmobranchs it consists chiefly of small yolk-spherules, and it is also Götte's floor of the germinal cavity (the "Dotterzellen"). In Teleosteans it is continuous with the peripheral wall of protoplasm (His's "Keimwall") and the thin periblast beyond, originating in the same way, and persisting probably by continual renovation, the blastoderm thus feeding upon this finely granular layer. Kowalewsky regards the intermediary layer as a provisional organ (*op. cit.*, 1886). We call by the name "subgerminal or nutritive disc" the disc-like stratum beneath the germ, and it embraces Lereboullet's two layers—the mucous and the oily stratum; it is the thin central part of Bambeke's intermediary layer; it is Oellacher's inner layer, holding many oil-globules, of the "Rindenschicht;" and although Oellacher speaks of it as more coarsely granular than the disc or layer above, yet it is derived from it. Oellacher rightly compares his lower layer to Lereboullet's mucous layer; while Bambeke also correctly says that both are really his intermediary layer.

We can therefore distinguish (with Bambeke) at the animal pole only two strata—

(1) the blastodisc, or true segmenting mass; (2) a granular layer, or subgerminal disc not segmenting, and probably nutritive, and interposed between No. 1 and the vitellus.

V. The Blastoderm.

Within one or two hours after the entrance of the spermatozoa, the thickened cap of protoplasm, either preformed as a discus proligerus, or segregated as a blastodisc proper, undergoes segmentation. The blastodisc is readily distinguished with the naked eye in the more transparent ova as a spot of lighter colour than the yolk on which it is placed; while under a lower power it is seen protruding as a discoid prominence at either the upper or the lower pole, according to the particular form. In certain Salmonidæ, for instance, the germ always floats uppermost, as it also does in the sterlet, according to Salensky, and in the trout; this being due, according to Ransom, to the oil attached to the disc, which compels it to float in the upper segment (No. 127, p. 450).* In a number of pelagic ova, possibly in all, the disc lies underneath the yolk, the animal pole being inferior; but whether superior or inferior, the position is constant for the species, and there is no actual reversal, such as occurs in Cephalopods, where the germ and the yolk-pole exchange places at a certain stage. As the vitelline mass revolves freely in the perivitelline fluid, the germ may often be brought to the upper side by agitation in the water; but it usually seeks the lower pole at once, and remains there when the egg is at rest.

Balfour views the disc merely as a part of the ovum, which is characterised by the presence of more protoplasm than the rest of the vitellus (No. 10, p. 106); but while this is so in the Elasmobranch and Amphibian ovum, in the Teleostei the germ is so well marked and distinct, and, with the exception of some colourless vesicles and a few granules, so destitute of yolk-matter (apparently consisting of pure protoplasm) that the yolk becomes rather an appendix than an essential part of the germ.

The same author supposed that the Teleostean yolk at some later stage must be almost entirely deprived of the protoplasm so abundantly interfused during the early stages, and this undoubtedly is so, the yolk-matrix before it wholly disappears increasing in density and coherency.† That the disc owes its origin to fecundation in all Teleosteans, we have seen to be an error; and the view of Coste, which Lereboullet adopts (No. 93, p. 33), is not more tenable—viz., that the disc is derived solely from the divided and scattered germinal vesicle—for, in some species, the discus proligerus is formed and this vesicle is seated in its midst. As the segregation of the disc proceeds, and its mass increases, its colour likewise becomes deeper; and Ransom believes that it undergoes a physical change, "being more solid" than in its earlier condition.

The disc then is the essential part of the ovum, and the yolk is merely supplementary,

* His figures the germ disc of *Esox* as uppermost (No. 67, Taf. i. fig. 13); but Lereboullet says, "Sa position est oblique ou, si l'on veut inclinée à l'équator" (No. 93, p. 481).

† In a form like *Anarrhichas* the embryo remains long (several months) within the ovum, and when treated with alcohol the yolk becomes extremely hard, and apparently consists of a purely albuminoid matrix. This likewise is the case with the ovum of *Salmo salar*. Sea water also hardens the yolk of the latter species (*vide* No. 104*a*, p. 153).

though the view is held by many authorities (Van Beneden, No. 25, pp. 52, 53; Hoffman) that segregation is equivalent to cleavage, and that when the disc is defined the ovum consists of two cells—one being the germ, and the other the yolk. The behaviour and undoubted function of the deutoplasmic globe is opposed to this view, the separation of the germinal matter from the inert yolk being protracted and undefined, and wholly unlike cleavage. Nor in the syncytial yolk has a nucleus been discovered equivalent to the segmentation-nucleus formed from the fusion of the male and female pronuclei in the germ. Dr Martin Barry, half a century ago (No. 21, p. 313), noted in the ovum of *Rana* a nuclear body, which he described as elliptical, well defined in contour, apparently granular, and placed within the membrana vitelli (*vide* Barry's figure, No. 21, pl. vi. fig. 28, *d*), but no such additional nucleus is apparently present in the Teleostean yolk.* The emphatically passive and inert character of the Teleostean yolk has already been indicated, and the real distinction of the active germ from its trophic appendage insisted on. We have referred to the relation of the early blastomeres and the potential yolk-segments Cunningham speaks of; but however plausible that view may appear during the first stages of cleavage, it is difficult to maintain such a relation of blastomeres and yolk when the morula is reached. The disc indeed becomes disengaged from the yolk (Gerbe says it completely separates, No. 57, p. 330), and a series of independent phenomena begin which concern it alone. We do not now allude to the formation of a true cavity beneath the disc, as this phenomenon falls to be considered later, but to the embryological separation between the germ and yolk, when their physical relations are most intimate. Cunningham (No. 48), referring to the statement made by Agassiz and Whitman (No. 2) that this separation dates from the 16-cell stage, observes, with greater accuracy than the two authorities named, that this separation by a cavity is not seen in living ova at the centre of the disc, and sections prove Cunningham to be right. In sections the line of demarcation is broken by knob-like processes which project from the blastoderm into the yolk (Pl. II. fig. 1), and these appear to be masses of protoplasm in the act of entering the disc, though another interpretation remains, viz., that they are pseudopodial protuberances.† During segregation and early segmentation remarkable changes of form are seen in the Teleostean blastodisc—similar to the phenomena Schenk noted in Elasmobranchs, and confirmed by Alex. Schultz (see Balfour, No. 10, p. 410), consisting of an alternate rhythmical pullulation and subsequent flattening or subsidence—a movement which involves the entire mass of the unsegmented disc (so that it seems to draw together and become compact and prominent). This is shared by the individual blastomeres in the segmented disc, as the separate cells appear at one time prominent rounded bodies standing boldly out upon the yolk, at another time as conical or irregular mounds (Pl. X. figs. 9, 10), or again flattened structures, crescentiform in section, their outline in the last case being less definite, and the entire disc exhibiting a diffuse and

* See Balbiani, *Comptes rendus*, 1864, tome lviii.

† Kowalewsky noted these transition-elements, and says that all stages can be seen amongst the entoblastic (yolk-mass) cells forming below the blastoderm—from those which are still in the yolk to those which had entered the blastodermic elements, and were only at one point of their bases united to the protoplasmic network of the yolk.

expanded appearance. These changes of external form, which are often combined with an apparent dehiscence of the blastoderm and puckering of the under surface (Pl. II. fig. 14), are probably due to the inherent mobility of the protoplasm; but are also connected doubtless with the transference of the cortical matter which has not yet ceased. They are especially noticeable when fresh cleavage is about to commence, as Ransom seems to have observed (No. 24, p. 466).

The primary segmentation-nucleus is rarely visible in the germinal disc,* though Kupffer noted it as a clear homogeneous vesicle, fifteen or twenty minutes after fertilisation, situated in the basal stratum of the blastodisc of *Clupea* (No. 87, p. 206). In the section of the blastoderm of *Gadus æglefinus*, at the 5th hour, when two blastomeres are completed, we see that the nucleus (*n*) occupies a position slightly above the basal stratum, and presents surrounding radial structures, apparently prolongations of the nuclear substance itself (Pl. II. fig. 18). When this nucleus has divided into two, each is seen to occupy a central position in the pair of newly-formed blastomeres. The two blastomeres (Pl. XXVIII. fig. 4) often show disparity in size, with a more or less distinct reniform outline when viewed from above. This disparity may be due to unequal segregation of protoplasm, or to more obscure causes, but the shape of the earliest blastomeres appears also to depend upon the direction of the first plane of cleavage; for, when this is in the shorter axis of the blastodisc, the two cells are rudely discoidal, and are in contact by their flattened margin; or if in the longer direction, the result, as in the gurnard, is the production of a pair of reniform cells—the hilum, so to speak, of each coinciding with the proximal margin. The nucleus in each blastomere is not spherical, but slightly elliptical and flattened, showing indeed as a transparent almond-shaped body, when viewed in profile, and of a paler hue than the surrounding matrix. In the living ovum the nuclei are usually very difficult to detect during the earlier stages, and Ransom failed to make them out (No. 127, p. 467); but, when not diaphanous, the nuclei may appear, *e.g.*, in the 2-cell stage of *Gastrosteus spinachia* and *Trigla gurnardus*, as minute irregular vesicles, like clear vacuolations distributed in each blastomere. The protoplasm around the central nucleus of each blastomere exhibits a radial disposition like the figure of the "lines of force" around a magnet (Pl. II. fig. 18), but the more detailed features of nuclear and blastomeric cleavage are of the complex nature characteristic of karyokinesis. Each cleavage begins as a superficial indentation, which in the case of the first furrow commences in the centre of the straw-tinted pullulation or granular blastodisc, within an hour or more from the first appearance of the disc, and extends outwards, its course being preceded by puckerings, as though the two masses were drawing apart, and producing the beaded structure described by Balfour (No. 11, p. 391). The diverging course of the cleavage-plane is not opposed to the "loi centripète" of M. Serres, for the plane penetrates (centripetally) the disc. The vacuolations which produce the beaded appearance, while most numerous at the margin of

* Ransom failed to make out the primary segmentation-nucleus, and indeed the blastomeric nuclei. Possibly various species may differ in regard to the visibility of the nuclei, for Lereboullet found the nucleus in *Perca* with difficulty, whereas in *Esox* it was well seen (No. 93, p. 513).

the cleavage-plane, occur sparsely over the disc, and especially in its basal portion (Pl. II. fig. 18). They probably have an important relation to the cleavage-process, as BALFOUR thought. In sections they occur as clear rounded vacuolations, but are without doubt filled with indifferent fluid, and probably are no other bodies than the clear vesicles scattered over the cortical protoplasm in the ripe unfertilised egg. The vesicles disappear, as we have seen, with the polar segregation of the disc; but they really persist, and are transferred to the disc, where they accumulate (Pl. II. fig. 18), often coalescing and forming larger vesicles, but not to be confounded with the oily extra-embryonic spheres, though LEREBOULLET does so, saying—"I have seen large transparent spaces like those M. VOGT shows in his figs. 113 and 114 (*Embr. of Salmon*) produced by oil" (No. 93, p. 486). It is possible that these vesicles, or rather their clear fluid contents, may render mechanical aid during cleavage, filling up with their less consistent matter the furrows formed by the dehiscence of the segmenting blastomeres. After the first furrow, which is perpendicular to the basal plane of the disc, has produced the first pair of blastomeres, the pullulation of the protoplasm is marked, each cell becoming increasingly definite, a feature which KUPFFER regards as indicating the appearance of an equatorial furrow (No. 87, p. 196, Taf. ii. fig. 15, &c.). Such an equatorial furrow, according to HOFFMAN, appears before the first perpendicular furrow, and thus the disc would be separated from the marginal protoplasm as well as from the yolk at the first stage in cleavage. A complete discontinuity of yolk and germ produced by cleavage does not accord well with the actual condition in the ovum, and the first furrow would appear to be the primary perpendicular one. When this furrow has penetrated almost to the base, for it does not perfectly bisect the disc, as LEREBOULLET long ago noticed (No. 93, p. 481; see his fig. 18, pl. i.), small furrows directed towards the centre of the disc, appear at right angles to the first cleavage-lines, followed by the appearance, along the course marked by them, of a second cleavage-furrow, which divides the two primary blastomeres into four almost equal segments. Each of the newly-formed blastomeres has a rudely square outline, its two free outer sides being rounded, while the two inner sides are more nearly straight lines, and mark the perpendicular planes which are in apposition to the similar surfaces of the two neighbouring blastomeres. In each blastomere a large nucleus can be made out, though often with difficulty, as LEREBOULLET noted; but not ill-defined, as the same author further stated (No. 93, p. 483), for the nuclei appear as homogeneous hyaline vesicles with a smooth and distinct contour, the bright contents of which are termed by AUERBACH the "ground substance"* (Pl. II. fig. 4, *a*). Nuclear division is not easy to follow in the living ovum, though blastomeric cleavage is readily observed. The ovum of *Esox* seems well adapted for nuclear observations, as LEREBOULLET found out when he contrasted this species with *Perca*, for in the latter the nuclei had greater transparency and were thus less readily seen (No. 93, p. 513). In this species (*Esox*) KUPFFER followed the division of the primary nucleus, and watched the first furrow pass down between the two newly formed nuclei (No. 87, p. 207).

* *Organologische Studien*, Breslau, 1873–4.

Around the cleaving nucleus a radial disposition of granules is seen,* the centres of the radii being the nuclear apices, for the nucleus itself becomes biconical and shows longitudinal striæ prior to the division which soon takes place across its middle or shorter axis, this transverse separation being followed by the division of the surrounding blastomere. The process indeed accords perfectly with Balfour's account of the Elasmobranch ovum (No. 15, pp. 394–5). Occasionally a blastomere is seen to contain two distinct nuclei, illustrating indeed the stage of the process figured in Pl. II. fig. 2, a stage which Lereboullet also clearly observed, for he says—"Dans un de ces lobes j'ai trouvé une cellule qui avait deux noyeaux distincts rapprochés l'un de l'autre" (No. 93, p. 484), and Balfour similarly speaks of a double nuclear condition (No. 11, p. 396). Though usually very distinct and centrally situated, the nucleus sometimes becomes diaphanous, and appears to be absent. Such an enuclear condition is hardly possible, though Professor Ray Lankester, it is true, speaking of the blastoderm of Cephalopods, says—"I have most fully satisfied myself that temporarily many of the segmentation-products are devoid of nucleus" (No. 90, p. 39); and Lereboullet, when noting the fact that all through cleavage each blastomere contains a nuclear body, adds that "often it may be absent" (No. 93, p. 484); while Bambeke could find no trace of nuclei in *Leuciscus rutilus*, but accounts for it by the similar refrangibility of the nucleus and the matrix in which it is situated (No. 20*a*). This disappearance of the nuclei is not an uncommon phenomenon in cell-division. Very often (Pl. II. fig. 1) a body apparently of the nature of a clear vesicle occupies the place of the deeply-stained nucleus in sections, or such a vesicle occurs only partly occupied by a nuclear remnant (Pl. II. fig. 1). These unstained bodies were noticed by Balfour, and he felt uncertain whether they were nuclei imperfectly stained, or nuclei in course of being formed (No. 11, p. 395). In the living egg the phenomena of segmentation are followed without much difficulty, especially in pelagic forms. The two primary cleavage-planes are seen to cut each other at right angles; but the third cleft is parallel to the second (Pl. X. fig. 4). On the completion of the third cleft the blastoderm consists of six cells, of which the central pair are larger than the others. At this stage the blastoderm is rudely rectangular, an outline altered by the next cleft, which passes once more parallel to the second and third clefts, through the large central cells (Pl. XIV. fig. 8). The size of the blastomeres is far from uniform after the 8-cell stage. The 16-cell stage is completed by a separate furrow traversing each cell and bisecting it, so that the total number of blastomeres is thus doubled at about the fourth or, it may be, the sixth hour after fertilisation. It would appear that in the Teleostean ovum, as also in the fowl and Selachian, the two primary furrows alone are really regular, the succeeding furrows being in varying degree irregular, so that the blastomeres are not seen to increase with the

* Oellacher observed the concentration of yolk-spherules round one or two centres in the segmentation-spheres, but this is not the phenomenon he described, though Balfour understood Oellacher to refer to the behaviour of the ordinary nuclei during segmentation. Ryder also speaks of numerous fine granules aggregated round two centres in the first cleavage-stage.

regularity of geometrical progression. The size of the blastomeres is likewise far from uniform after the 8-cell stage, and in the 14- to 16-cell stage especially, they vary very much in size and shape, the outer being large and somewhat rectangular, while those more central are smaller and ellipsoidal. This distinction between the more external and the inner cells Balfour noted in Elasmobranchs (No. 11, p. 392), and compared it to the horizontal furrow which separates the smaller pigmented spheres from the larger spheres of the vegetal pole in *Rana* (*cf.* figs. 3, 4, and 5, pl. xv. No. 11, and our Pl. IX. fig. 8). The form of the disc varies, changing from the circular outline of the early blastodisc (Pl. XXII. fig. 1) to a more or less regular quadrate figure (Pl. X. fig. 9), and reassuming the circular form when the multicelled stage (morula) is reached (Pl. II. fig. 13, *a*). The first furrow parallel to the base of the disc passes across the median horizontal plane at about the 50-cell stage (Pl. II. fig. 14), and the subsequent cleavage becomes very complicated. Owing to the increasing pressure of adjacent cells, the rounded form of each cell (Pl. X. fig. 10) becomes altered, and the polygonal shape is assumed (Pl. II. fig. 19). The size of the blastomeres shows much variability, though the variation is now within narrower limits. In profile the disc up to this stage has maintained the plano-convex outline, which is often retained until the 180-cell stage or later (Pl. X. fig. 10); but when the cells are so subdivided as to appear almost of one size, a marked bi-convexity is assumed, and upon the yolk a depression is formed in which the blastoderm rests (Pl. II. fig. 2), as it does permanently in Salmonoids (Lereboullet, No. 93, p. 485; Oellacher, Klein); but later it spreads out in Gadoids and other forms, and appears as a flattened plaque in which several layers of similar cells can be distinguished (Pl. II. figs. 3 and 15, *e*). There is no marked difference in the cells of the various strata, and the blastodermic layers are not readily distinguished, as they are in Elasmobranchs.* Balfour and other investigators have made allusion to this similarity in the size and contour of the cells of the Teleostean blastoderm (*vide* Balfour, No. 11, p. 551; and Lereboullet, *op. cit.*).

It is true, as already pointed out, that in very early cleavage the marginal cells are distinguished from the inner cells by a marked difference in size (Pl. IX. fig. 8); nor is the distinction lost with the appearance of the horizontal furrows, though it cannot be due, as is undoubtedly the case in Elasmobranchs and Amphibia, to the greater proportion of yolk-matter present in the outer germinal protoplasm, for there does not appear to be any conspicuous difference in their physical character.

In the Elasmobranch blastoderm of about one hundred cells, the ectoderm is readily distinguished from the endoderm or "lower layer" cells by their smaller size, and marked columnar character. Rieneck† observes that the upper cells of the germ give rise to a two-layered sensory lamina (or leaf), and that some of the lower cells fall to the bottom

* Ryder, however, speaks definitely of three layers in the multicelled stage of the Teleostean germ; but this does not agree with other descriptions by the same author.

† *Archiv f. Mikr. Anat.*, vol. v., 1869.

of the cavity (germinal cavity). Soon after also the larger cells fall off, and we now get complete analogy with the Amphibian egg, viz., above the cavity the sensory layer composed of smaller cells, and below the large cells for the body of the embryo.* This is not the case, however, in osseous fishes, for on the completion of segmentation, an epiblastic layer can barely be distinguished: it is not by any means well marked.†

Germinal Cavity.—With the completion of segmentation the blastoderm undergoes a change of the most striking character. It lengthens out (Pl. II. fig. 17) and soon becomes elevated from the yolk, so that a chamber *gc.* (Pl. II. fig. 15, *a–d*), not coincident with the centre of the disc, is formed between its under surface and the vitellus (*y*) below.‡ Hitherto the whole of the inferior face of the blastoderm has rested immediately upon the yolk (*y*) (see Pl. II. figs. 1–3) or rather upon a portion of the yolk-cortex; but now the inner surface being raised it rests only by its periphery, and the eccentrically situated cavity intervenes between it and the vitelline mass. In *Trigla gurnardus* the sub-blastodermic cavity is plainly visible on the second day, when the germ covers barely a third of the surface of the yolk.

A cavity has been observed in some Teleostean ova at a much earlier stage; but it is probably a precocious dehiscence and of minor significance. Such a cavity in the gurnard may be formed even before the first cleavage is accomplished, and is probably due to the cleavage-process, as we find to be the case in *Amphioxus* at the 4-cell stage. Agassiz and Whitman found a similar cavity in *Ctenolabrus* at the 16-cell stage, while His describes one at the 8-cell stage.§ Such cavities, of a transitory nature, have been noticed in very many ova; in *Acipenser sturio*, for example, at the 6- to 8-cell stage, according to Kowalewsky, Owsjannikow, and Wagner; while Rauber saw it in the Avian ovum at the 4-cell stage (No. 132, p. 6). The last named observer distinctly affirms that the early cavity he saw is not the homologue of the later embryonic chamber, generally distinguished as the "Keimhöhle;"‖ and as this is a point of no little importance, it is desirable to dwell upon the distinction here implied. The very existence of a cavity, either "segmentation" or "germinal," has been denied by some investigators. It has been pronounced by Donitz amongst others (No. 52, p. 600) to be merely an artificial product; and Kupffer suggests something of the same kind, though unwilling to lay stress upon his results, which were negative (No. 87, pp. 214–16). That the somewhat complex methods now adopted in laboratory work are calculated to produce occasionally artificial changes in embryonic

* Rieneck also considered that the embryo originated in one point of the peripheral thickening which occurs at the point of contact between the yolk and the germ.

† Goette affirms that there is no distinct differentiation of any of the germinal layers in the multicelled condition of the disc if we except the outer "epithelial" (*Archiv f. Mikr. Anat.*, iv., 1868).

‡ Rieneck, *op. cit.*, observed the central part of the germ lifted off its underlying part.

§ It is this cleavage-cavity which Ryder considers as probably homologous with the cavity of the false amnion (*Amer. Nat.*, xix., 1885, and *Jour. Roy. Micr. Soc.*, Feb. 1886, p. 45).

‖ This later cavity Balfour, in common with most observers, names the segmentation-cavity, though he says it is not a well-defined chamber, and remarks that "it may even be doubted whether a true segmentation cavity . . . . is present."

structures is very probable; but the recognition of a cavity in the Teleostean blastoderm has been so general that it cannot be placed in such a category.

We speak of it as a "germinal cavity," and do so advisedly, for it is not "the cavity of Von Baer," better known as the blastocœl or segmentation-cavity. This latter, which exists in all segmented germs forming a blastosphere, as in Cylostomes and *Amphioxus*, is, we believe, never formed in such pelagic ova as are referred to here, nor indeed has it been clearly recognised in any other Teleostean ova, with the exception of *Leuciscus rutilus*. In this last named ovum Van Bambeke fully describes a true "segmentation cavity," though his results are not in accordance with those of embryologists generally. Van Bambeke himself doubts the existence of his cavity in the germ of the Salmonoids and carps, though closely allied to the form he investigated, and declares it to be homologous with the chamber in the ovum of *Petromyzon*, *Acipenser*, the Selachians, and Amphibians. It is true he quotes Lereboullet in support of his view, and the latter undoubtedly does speak of the germ at the close of segmentation as having "un aspect granuleux et la forme d'une sphere aplatie qui repose sur le vitellus" (No. 93, p. 503); but neither his fig. 27, pl. i. nor fig. 3, pl. iii. necessarily imply Bambeke's results, nor exclude the existence of the germinal cavity which most authors have seen. The segmentation-cavity of Bambeke, the homologue of Balfour's cavity (No. 13, pl. xxi. fig. 1, *sc*), arises as a space in the midst of the blastodermic mass (No. 20*a*), at what period he cannot say, though his figure would indicate an early stage, probably when the blastoderm covers a quadrant, that is at the same time as the "germinal" cavity, which it also resembles in its non-central position, for it is slightly eccentric in position, and in front of the embryonic area proper. It is surrounded by blastomeres—the roof, walls, and floor being composed of cells produced by the segmentation of the disc. The germ, in which it originates, is essentially a blastosphere, for though the floor-cells largely disappear, so that the yolk may seem partially to form the floor, there is probably never a stage, as Balfour is careful to note (No. 11, p. 519), "in which the floor of the cavity is without cells." Balfour, it is true, regards the Teleostean germinal cavity as homologous with the segmentation-cavity (cavity of Von Baer) in Elasmobranchs and Amphibians (No. 10, i. p. 70); but the subsequent fate of each of these cavities tells against this homology, for the former is persistent, whereas the latter chamber is transitory. If the Teleostean germ after segmentation be a morula, which flattens out, and becomes lifted up, and separated by a chamber from the appended trophic mass,* resembling in a remarkable manner the condition in certain Urochordates (*e.g.*, the cauducichordate *Pyrosoma*), in which no centrally placed segmentation-cavity occurs (*vide* Huxley, No. 73, and Kowalewsky, No. 86, p. 609), then the presence of such a cavity, and the occurrence of a blastospherical stage in Teleosteans, must be regarded as problematical.

* That the blastoderm is actually raised up seems to be demonstrated by the fact that separation may for some time be incomplete, connecting strands of protoplasm being frequently distinguishable in the living ovum and in sections (Pl. II. fig. 15, *c*), and Ryder is probably in error when he supposes the cavity to arise as a direct result of cleavage (No. 141, p. 492).

Balfour at one time held the view that the floor of the cavity in Selachians was not truly blastodermic, the floor-cells arising as concretions around yolk-nuclei at the base of the disc (No. 11), and such a cavity would be a germinal, not a segmentation-cavity like Van Bambeke's; but later, Balfour relinquished this view, a complete floor being established, he states (No. 11, p. 43), by the growth inward of lower layer cells along with cells formed in the periblast. The cells which Oellacher describes on the floor of the "Keimhöhle," he says fall from the roof of the cavity, sink into the yolk, and multiply (*Zeitsch. f. w. Zool.*, xxiii. pp. 12, 13). The real nature of the blastodermic vesicle of Lereboullet is by no means clear, for though Bambeke regards Lereboullet's cavity as no other than his own, yet it must be remembered that Lereboullet's mucous layer is not necessarily a blastodermic layer in the strict sense; and Van Bambeke himself admits this possibility when he points out the likeness of this layer with his intermediary layer (No. 20*a*, p. 4), a point E. van Beneden also insists upon. That Lereboullet himself regarded his "feuillet muqueux" or "végétatif" as extra embryonic, is clear from his denying that it is formed of blastomeres —"in fishes and Crustacea (the crayfish) the mucous layer," he says, "is not of the same origin as the serous layer" (No. 95, p. 14), the one being the true or animal blastoderm, and the other the nutritive blastoderm.* It is not necessary here to decide the real nature of the mucous layer, whether it be truly hypoblastic, or hypoblast and mesoblast, or neither; it is sufficient to note that the floor of the cavity, according to Lereboullet, has a different origin from the roof, and is not composed of cleavage-products, so that his cavity would not seem to be a segmentation cavity at all, and though he considered himself justified in stating that the blastoderm is "creuse et forme unevéritable vésicule . . . . dont les parois sont plus ou moins rapproches l'une de l'autre" (No. 93, p. 487), yet it must not be regarded as the segmentation-chamber of a blastosphere, but the germinal-cavity underlying a morula. If Oellacher be right, that only cells resulting from cleavage form the blastoderm, then a cavity, if not floored by such cells, is not a segmentation-chamber according to the accepted view regarding that cavity. The nature of the floor of any cavity appearing in an early blastoderm is all important, while the nature of the roof is not so, being, indeed, subject to variation in very closely allied forms like *Rana* and *Triton*, one layer of cells forming the roof in the latter (No. 147, p. 453), whereas in *Rana* the roof is two or more cells thick. The lamprey has a multicelled roof, which thins out to a single layer, as Shipley has found, in agreement with Calberla, and as opposed to M. Schultze; whereas in Elasmobranchs, as also in Ganoids (*Acipenser*), the ectodermic roof is thickened by endodermic cells which creep up the walls of the cavity and pass along the roof. The roof of the germinal cavity in Teleosteans is formed by the whole of that portion of the blastoderm which is raised to form it (Pl. II. fig. 15*b*, *bdm*). It therefore includes epiblast (or ectoderm) and lower layer or

* That Lereboullet's upper layer cannot be the epiblast, and his second layer the entoderm or "lower layer cells," is shown by the fact that he speaks of the lower as a single layer (No. 93, p. 492), and the upper as of many regular layers of smaller cells, so that our interpretation holds best.

endodermic cells. When at its maximum it is a slightly flattened dome-like cavity (Pl. II. fig. 15*b*, *ge*); but with the extension of the blastoderm its roof is depressed, and it thus appears subsequently as a mere fissure. Now Lereboullet figures his cavity as a narrow fissure extending almost from margin to margin of the blastoderm; whereas Bambeke's is a compact, but loftier and more spacious chamber.* It is noteworthy that Bambeke was struck by this dissimilarity, and after examining the segmentation-cavity in the roach was prompted to seek for a germinal cavity underneath the blastoderm, and found one, as he indicates in his figs. 4 and 6 (*vide* No. 20*a*); but he adds that "a comparative examination of preparations forces me to regard it as a simple accident and artificial, for the prominences and depressions of roof and floor coincide." There is much reason to suppose, therefore, from the shape and nature of the floor, that Lereboullet's cavity is not a segmentation-cavity, such as Bambeke supposes, and, if this be so, then Lereboullet likewise discovered this flattened germinal cavity, as E. van Beneden says (No. 25, p. 47), though this author is wrong in according the discovery also to Van Bambeke. If, on the other hand, Lereboullet's be really Von Baer's (and Van Bambeke's) cavity, then H. Rathke first signalised the germinal cavity in *Zoarces;* and he was followed by Stricker. It is therefore not correct to speak of a cavity of Lereboullet with Van Beneden but rather of a (sub-blastodermic) germinal cavity, which is persistent through all embryonic life, as distinct from the (intra-blastodermic) segmentation-cavity which wholly disappears.†

What then is the significance of the germinal cavity thus distinguished? By the fact that its floor is formed of yolk, or rather the protoplasmic cortical film (or intermediary layer), and that it is roofed over by endoderm (lower layer) and epiblast-cells, it is comparable to the "Keimhöhle" in the fowl's ovum.‡ At a later stage the hypoblast-cells which intrude from the periphery to form the blastodermic rim (*br*) and shield (Pl. II. figs. 15, *a*–*e*, and 17) do not pass across the floor of the cavity, but creep up the sides and partially arch it over, forming in fact a gastrula which would open externally by the blastopore, were not this aperture plugged up by the mass of yolk (really Ecker's plug), which is so large that the invaginated lip is compelled to pass round, and epibolically envelop it. The germinal cavity, arched over as it is by the thick blastodermic roof, *bdm* (Pl. II. fig. 15, *a*–*e*), is never truly open in the sense indicated; but potentially it is so, the removal of the concentrated trophic matter (*y*) which does not segment would leave the blastoderm a simple gastrula—indeed, as Ryder remarks in regard to *Alosa*, that "the yelk might be removed at any stage without taking away any essential part of the embryo except the floor of the cavity" (No. 141, p. 569). Van Bambeke does not hesitate to regard his chamber as a gastrula-cavity, and finds in it therefore great phylogenetic

* A glance at Lereboullet's figure (No. 93, pl. iii. fig. 3) and Bambeke's (No. 20*a*) sufficiently shows this.

† See a paper "On the Significance of the Yolk in the Eggs of Osseous Fishes," by E. E. Prince, *Ann. Nat. Hist.*, July 1887.

‡ It is interesting to observe that, with the appearance of the germinal cavity, the thick periblast-floor in some forms becomes thinner. The Keimhöhle or germinal cavity is often called the segmentation-cavity in the fowl's ovum.

significance; but Oellacher, Donitz, Ryder, and others agree that it is merely an artificial product, and due to the action of reagents. It is difficult to accept the latter view, after the careful observations of Van Bambeke, who admits that in the trout and carp it is absent, as seems to be also the case in a large number of Teleosteans at St Andrews; yet since a cavity of this nature, remarkable for its deep situation and transient nature, has been seen in other blastoderms (*e.g.*, Aves and Ganoids), it may justifiably be regarded as a normal structure, and perhaps due rather to the exigencies of the cleavage-process than to ancestral causes. If, as Whitman holds (No. 159, p. 296), "the case of *Ascidia* (Kowalewsky), of *Sycandra* (Schultze), of *Anodonta* and *Unio* (Flemming), of *Clepsine* and *Euaxes*, and numerous cases like the latter, show that the blastocœl arises by the cells being pushed asunder in the process of cleavage," then the segmentation-cavity when it is present can have no profound ancestral meaning, such as Van Bambeke urges; but is of interest merely in connection with modifications in the ovum, by which the area embraced in segmentation is greatly reduced. This reduction implicates a mechanical difficulty, resulting in the formation of a chamber, which is appropriately named a segmentation-cavity or blastocœl. Probably every instance of a blastocœl may be explained in this manner, and it may thus co-exist along with the germinal cavity. The former, it is generally admitted, becomes obliterated, whereas the latter persists, and must be regarded as the remnant of the primitive enteron. Its persistence in the embryo is of importance, for it is an essential point in the gastrula that "it should directly or indirectly give rise to the archenteron" (No. 10, p. 457). That in forms so various as *Gallus*, *Rana*, *Acipenser* (No. 82), and *Balanoglossus* the segmentation-cavity is transient, and has no relation to the blastopore, is proof that it cannot be regarded as enteric, for the archenteron has always relation to the blastopore. In speaking of the cavity in the Teleostean ovum as germinal, we merely do so to distinguish it from the segmentation-cavity (blastocœl), which is wholly another structure, though the name does not necessarily imply any ulterior meaning. Nor is this course discordant with the conclusions of Teleostean embryologists in general: for Oellacher distinctly affirms that the germinal cavity produced by the lifting up of the germinal mass is the sole cavity observed by him in *Salmo fario*, and he failed to find a central segmentation-cavity, as was the case also with Van Bambeke in the ova of this species, and of *Cyprinus;* and Klein, though he speaks of a segmentation-cavity, formed by the lifting up of the blastoderm, really means the germinal cavity (No. 79, p. 197, and pl. xvii. figs. 11 and 12), this latter cavity being also recognised by Rieneck (No. 137, p. 356), Götte, Henneguy, Owsjannikow, and Weil. Janosĭk observed a cavity in the germ, and an earlier one between the yolk and the lower layer cells, and he termed the former "segmentation-cavity."* It is not a little curious that Ryder, while holding that the germinal disc of Teleosteans is equivalent to the entire Amphibian ovum, yet regards the cavity outside the disc (germinal cavity) in the former as homologous with the deeply placed chamber (segmentation-cavity) in *Rana* and the

* *Archiv f. Mikr. Anat.*, vol. xxiv.

Elasmobranchs, and somewhat inconsistently maintains that in Teleosts the origin of the cavity is directly due to cleavage; whereas, on phylogenetic grounds, it must arise in connection with the peripheral invagination and the formation of the blastopore. If, as Ryder holds (No. 141, p. 492), the Teleostean germ is equivalent to the whole ovum of *Rana*, then we must look for a segmentation-cavity deeply placed in the former blastoderm, a fact which Bambeke, as we have seen, considers established for *Leuciscus*. Ryder, too, adopts a questionable view of the germinal cavity, when he says that it is "simply a space filled with fluid, which facilitates the gliding of the blastoderm over the yelk during growth," and constituting the fissure between the outer (embryonic) layer and the inner envelope of the yolk, and further as the representative of a "primal nutritive space," a lymph-cavity. He also considers that the body-cavity is continuous with the segmentation-cavity, and maintains that it does not disappear in *Gadus morrhua*, *Cybium*, *Coregonus*, and *Alosa*.

While there are many points, therefore, which support the view that the segmentation- and germinal cavities are not one, but may indeed co-exist, or may appear successively in the same ovum, there is a possibility that the difference between the deep-seated cavity, seen, for example, in Elasmobranchs, and the sub-blastodermic chamber in Teleosts, may, with extension of our knowledge of the early blastoderm in the latter, disappear, and this would be so if it could be shown that the germinal cavity arises, not by the lifting up of the disc, but by intracellular dehiscence, and the disappearance of the lower (separate) stratum, *i.e.*, the blastomeric floor.* At present the germinal cavity must be distinguished as such, the characteristic features being its situation superficial to the yolk, the absence of blastoderm-cells separating it from the granular yolk-cortex, and its persistence even into the later embryonic period. Other minor features justify us in emphasising the distinction of this cavity from the blastocœl or segmentation-cavity proper.

VI. Periblast or Nuclear Zone.

From the way in which the protoplasm of the ovum collects at the animal pole, it is readily seen that the continuity of the disc and the cortical protoplasm beyond does not cease for some time, and that even when the blastoderm by cleavage has become defined in the form of a cellular prominence, its connection with the unsegmented protoplasm external to it is most intimate. The process of superficial transference still proceeds after cleavage has commenced.†

* The fact that during a considerable interval the segmentation-cavity in Elasmobranchs is greatly deficient in its cellular floor, and the yolk limits it below (No. 11, p. 518), is interesting, though Balfour doubts if ever the yolk alone forms the floor (p. 519). Götte's observations would demonstrate the existence of such a floor of cells in the Teleosteans, though it is always incomplete.

† Granular yolk is also transferred in the Elasmobranch, both Oellacher and Balfour agreeing that yolk is assimilated by the germinal area during segmentation. The cessation of the transference and of the yolk cell-gemmation accounts in a great measure, according to Balfour, for the comparative distinctness of the disc and the yolk at the end of segmentation.

So long as the yolk-ball can be distinguished even in advanced embryonic stages (see Pl. VII. figs. 1, 9, &c., *cp*), it is provided with an envelope of unsegmented protoplasm especially noticeable round the margin of the disc (*per*, Pl. II. fig. 12), and forming in the early stages of cleavage a thickened peripheral belt. This envelope is the "feuillet végétatif ou muqueux" of Lereboullet (No. 93, p. 771); the "trophic or glandular layer" of Remak (No. 135, p. 342); the "parablast" of Klein (No. 79, p. 116) and His (No. 67); the "Korner-zone" of Kupffer (No. 88, p. 217, fig. 1); the "lamina mycogastralis" of Haeckel (No. 62); and the yolk-hypoblast of Ryder (No. 141); but appropriately distinguished as the "periblast" by many authors.

We may speak of the periblast as early as the stage of first cleavage, the two primary blastomeres constituting the germ proper as distinct from the protoplasmic layer beyond.* The distinction, it is true, is more apparent than real, for the protoplasm at the margin of the disc is in a state of continual transition, passing into the germ probably during the whole cleavage-process, the disc being indeed only a thickened portion of the protoplasmic cortex of the egg,—"a lenticular enlargement of the Rindenschicht," as Oellacher expresses it (No. 113). In thus regarding the periblast as an aggregation of protoplasm which lies outside the germ proper, because it has reached the animal pole too late to enter the disc and take part in cleavage, we adopt a theory of its origin which has been questioned by some observers, notably by Agassiz and Whitman (No. 2). These observers suggest that the periblast is really a product of the blastoderm; that, instead of being, as we have expressed it, too late to enter the disc, it has already formed part of that structure, and has been protruded as a germinal outgrowth all round the margin during segmentation. Van Bambeke, as if by anticipation, expressly opposes such a view, and says—"It cannot originate from the disc; it is coarsely granular, like the cortex (le manteau protoplasmique);" but he goes on to state that the cortex wholly disappears when the intermediary layer is formed, whereas the cortex persists very much longer, though so thin that, as he says, "it is difficult to detect" (No. 20*a*).

It is not easy to controvert a view which denies the independent origin of the periblast, for its apparent extension outwards from the margin of the disc and the continuity of both would seem to favour it. But, if it be correct, then at one stage all the superficial protoplasm of the ovum must be collected into the germ-mass; and no such complete segregation has been observed—a stratum of cortical protoplasm continuous with the germ is always discernible up to the stage when the periblast can be distinctly recognised as a nucleated layer. Its extension beneath the disc is implied in the view here adopted, for the superficial protoplasm collects beneath the disc as elsewhere, and this can be observed by the behaviour of the oleaginous sphere in such an ovum as that of *T. quercardus*, inasmuch as it passes along beneath the floor of the germinal cavity evidently prevented by the layer of continuous protoplasm from entering the chamber. Van Bambeke, it is true, questions this latter point, saying that at one time no trace of a

* Kingsley and Conn, in mentioning that complete furrows in segmentation pass downward to the vitelline globe, except the intermediary layer and peripheral cushion of Van Bambeke. We agree with this view.

central lamella can be seen, and that it is "most probably formed by extension under the disc from the bevelled ring outside." Like AGASSIZ and WHITMAN, LEREBOULLET holds that this layer is formed later than the disc, observing that, "at the close of segmentation, no trace of the mucous layer is seen, though dispersed vitelline globules are visible out of which this layer is formed" (No. 93, p. 495).

Three theories of the origin of the periblast are thus held—(1) that it is simply a separation, a superficial segregation of protoplasm interfused in the yolk, and reaching the animal pole too late to enter the disc; (2) that it does form part of the disc, but afterwards issues from it all round the margin, extending as an extra-germinal layer; (3) that it is not a mechanical transference, but an actual transformation of yolk-particles. The second and third views, just stated, involve processes less simple than the first, and if a process of simple transference, the segregation of interfused germinal matter, suffice, it is needless to resort to any explanation more complex. The superficial segregation of protoplasm implies that a sub-blastodermic stratum is never wanting, and that, from the first, the blastomeres "do not rest" (in E. VAN BENEDEN'S words) "immediately on the vitellus; they are separated from it by a layer of substance which is finely granular" (No. 25, pp. 44, 45).

For some time the periblast remains homogeneous, devoid of nuclei, and not separable from the yolk-cortex beyond, save by its slightly greater thickness (*per*, Pl. II. fig. 14), and by the occurrence of scattered granules in it, which are distinctly seen at the end of the first day in *G. morrhua*. Further, the occasional presence of protoplasmic filaments over the area of the periblast seems to indicate its tenacious character (Pl. II. fig. 7). It forms in some ova, as LEREBOULLET and E. VAN BENEDEN noted, a considerable thickening below the centre of the germ. This thickened central lamella disappears later, and it is doubtful whether in many species it is ever present. The peripheral thickening is usually well marked* as a prism-shaped ring (*per*, Pl. II. figs. 1–3), which is triangular in cross-section, the disc resting upon one side, the lowest side being in contact with the yolk, while the third is external and free. When segmentation is far advanced and the biconvex form has been assumed, large nuclei begin to appear in close proximity to the margin of the germ (Pl. IX. fig. 10, *n*). Though irregularly disposed, two or three rows may be distinguished (Pl. IX. figs. 9 and 10, *n*; and Pl. II. fig. 4*a*), and they rapidly extend outwards over a variable area, which is known as the nuclear zone. The nuclei are large clear vesicles, having a slightly pinkish hue in certain lights (transmitted), well-defined and rounded in form, often slightly elliptical, and showing in some cases granules or nucleoli (Pl. II. figs. 6, 8, *n*; and Pl. IX. fig. 9). At first they are crowded together, but as they extend towards the equator they show a tendency to a regularity of disposition which is very remarkable when they are five or six deep. KUPFFER describes these bodies in certain species of *Gastrosteus* as larger than the nuclei of the germ, separated by regular intervals three times the diameter of each nucleus, and arranged in rows duly alternating, the row nearest to the

* LEREBOULLET descants upon its unusual thickness in the trout (No. 95, p. 14).

disc being the first to appear, the rest following in succession (No. 88, p. 217). At the 12th hour, in the gurnard, the nuclear zone forms a conspicuous spotted belt round the disc, and the yolk in certain views seems to be distinctly pitted by them (Pl. II. fig. 5). A little later they are less distinct. When the blastoderm has extended over one-third of the yolk-surface, traces of the nuclei are still to be seen (Pl. XIV. fig. 7, *np*). Thus, at the 25th hour, in the gurnard the blastoderm is surrounded by a continuous belt of protoplasm, beyond which few or no granules exist. Those previously seen have been overlapped by it, but are visible underneath towards the rim. In the surrounding protoplasm no large nuclei appear, and only a few of the granules of the previous stage. Often, during the early period of the nuclear zone, the nuclei appear in groups as if multiplying by division, this being well marked in the ova of *Gadus morrhua;* but on the second day the nuclei are invisible, and only a granular ring surrounds the disc.

How do these nuclei arise? Three possible geneses are suggested,—they may be derived from the nuclei of the blastoderm, as Schultze, Oellacher, Whitman, and Wenckebach (No. 158)* hold; or they originate directly or indirectly from a primary yolk-nucleus (Hoffman, E. van Beneden); or lastly, they may be endogenously formed as independent segregations of active protoplasmic particles (Kupffer), either from the marginal cells, or from the cells which fall from the lower surface of the "segmentation-cavity," or rather germinal cavity, and which fuse with the periblast. Wenckebach asserts that no nuclei or cells arise either in the periblast or in the yolk, and that the nuclei of the periblast, after their separation from the blastoderm, degenerate and take no part in the formation of the embryo.† The appearance of the extra-embryonic nuclei later than the nuclei of the germ—further, their first manifestation close to the margin, and their increase centrifugally from the blastoderm, point, it cannot be denied, to a blastodermic origin. Their derivation from an original single yolk-nucleus has not been demonstrated by any observations, nor does it appear to be supported by the manner in which the nuclei become visible, though it accords best with the theory that the multinucleate condition is less primitive than, and derived from, the uninucleate. This contention Butschli has devised, and he adduces the case of certain Infusorians in which not only is the multinucleate condition prior, but actually gives rise to the uninucleate condition—many nuclei coalescing before nuclear cleavage takes place (No. 36, pp. 212–13). It must be observed, on the other hand, that Englemann (No. 54, pp. 576–7) and Zeller (No. 161, p. 360) have shown that in *Opalina* the multinucleate is unmistakably derived from a primary uninucleate condition. The existence of a primary yolk-nucleus in Teleosteans still remains to be demonstrated. If, by segmentation of this nucleus, the periblast-nuclei are produced, appearances in the living ovum afford little evidence of it; but if the nucleus dissipates, and later, becomes aggregated again at numerous superficial centres, then this view is not without support.

Kupffer, Klein, and other authors regard the nuclei we are considering as free

* Ryder recently adheres to this view (*U. S. Com. Report for* 1885 (1887), p. 490).

† No. 158, and *Jour. Roy. Micr. Soc.*, Feb. 1887, p. 43.

nuclei, originating as independent segregations of active protoplasm, like the nuclei which arise endogenously in the Molluscan ovum, as Professor RAY LANKESTER was the first to recognise. In Crustacean ova such nuclei have long been known, though in *Oniscus* it is noteworthy that BOBRETZSKY affirms their blastodermic origin and subsequent migration; but this view is not generally accepted. WEISSMAN, too, imagined that in the ova of Dipterous insects such structures arise *de novo*, and without genetic relation to nuclei already existing; but later researches lend little countenance to this opinion, and WEISSMAN has abandoned his contention. KOWALEWSKY has described in the yolk-matrix of the Annelidan ovum scattered nuclei, endogenously formed and afterwards collecting superficially, especially beneath the blastoderm; they are at first few in number, but show rapid increase, and are especially abundant about the time of exclusion. He regards the nuclei of the "intermediary layer" in the Teleosteans as originating from those of the entoblastic (yolk-) cells. The appearance of free nuclei in the region outside the embryonic area in the chick, as described by RAUBER (No. 133, p. 570), is a further instance of such extra-embryonic nuclear bodies, and the nuclei in the Teleostean periblast may have a like origin.* The fact that they differ in shape from the spherical nuclei of the disc—being generally more or less elliptical, and often of larger size (Pl. II. fig. 6, *n*)—points to a non-blastodermic origin. KUPFFER speaks of their differentiation, and of delicate contours which appear round them resembling hexagonal figures, in *Clupea* (No. 87, p. 205). LEREBOULLET observes that they are large and granular in *Esox*, and along with the matrix in which they lie, they "come from another source" than the protoplasm and nuclei of the disc (No. 93, p. 494). BALFOUR, again, comes to the conclusion, while leaving their origin an open question, that there is no evidence of their derivation from pre-existing nuclei in the blastoderm (No. 10, p. 109).

In the living Teleostean ovum it is difficult to watch the actual formation of these nuclei; but KUPFFER describes with some detail the appearance in *Clupea* of clear spots of protoplasm which grow from a speck-like particle to a body 5–6 μ in diameter (*op. cit.*, p. 201), and E. VAN BENEDEN† is no less decided in affirming that these nuclei arise "par voie endogene" simultaneously in the periblast. We have noted that in the egg of the cod, towards the end of the first day, the periblast shows only minute granules scattered through its translucent protoplasm. The nuclei‡ are few at first, and close to the edge of the disc, as if some of them had escaped by "hernia." At other parts of the periblast clear vesicles and minute granules occur. Observations do not strongly support the view that the nuclei of the periblast migrate from the archiblast, but probably they arise in the periblast itself, and it may be that the activity in the disc proper stimulates similar activity in the periblast, just as a limited area of irritation in

* RYDER regards the "nuclear zone" as homologous with this germinal wall in the chick, and it is certainly noteworthy that the nuclei in the latter (the "white yolk nuclei") are most abundant below the thickened periphery of the blastoderm, and become the nuclei of cells which enter the germ. † *Belg. Acad. Sc.*, No. 6, June 1876, p. 1202.

‡ KINGSLEY and CONN (*op. cit.*, p. 199) observed in the cunner the formation of cells round these nuclei on the surface of the yolk; but it seems, according to Mr G. BROOK, that Mr KINGSLEY has since altered this view (*Trans. Roy. Soc. Edin.*, 1887, p. 224).

ordinary vertebrate tissues has a tendency to stir up a like condition in surrounding parts. So early as the 32-cell stage in *T. gurnardus*, numerous nuclei, precisely like those afterwards present in the periblast, were observed, irregularly scattered beneath the blastoderm. Some of these nuclei, which were in close proximity to each other, coalesced and formed large irregular structures.

On one occasion careful focussing brought out beneath the cells of the blastoderm (in an ovum of the species just referred to, of which the yolk was about half enveloped) the faint outlines of periblastic nuclei, while, in an oblique view of the invaginated rim its under surface was somewhat regularly nodulated by the nuclear projections which thus protrude into it from below (Pl. II. fig. 5).

The blastoderm of *Gastrosteus spinachia* at a certain stage shows, scattered throughout its extent (Pl. II. fig. 9, *n*), large bright nuclei, often showing many nucleoli. These nuclei, as suggested elsewhere (No. 124, p. 493), are probably periblastic, and they persist for some time after the closure of the blastopore.

After their appearance close to the margin of the disc, they extend outwards, while at the same time they also pass inwards, and form a nucleated stratum beneath the blastoderm. They progress centripetally, and eventually stud the periblast-floor of the germinal cavity, and are visible through the roof formed by the translucent blastoderm; but whether they increase by cleavage or spontaneous endogeny is not clear. Balfour states that they increase by division (No. 10, p. 109), and nuclei frequently show a transverse line coinciding with the short diameter (Pl. IX. fig. 10), but the further constriction and "direct" division of an example of such nuclei into two daughter-nuclei was not made out,* and it is probably true that they arise and multiply precisely like the nuclei named "autoplasts" by Professor Lankester in the ovum of Cephalopods—arising and multiplying not by cleavage, but originating *de novo* as independent segregations.†

The behaviour of the nuclei outside the disc in Teleostei is similar to that in Elasmobranchs, as Balfour clearly states that whatever influence the nucleus may have in ordinary cases of cell-division, it may yet undergo precisely similar changes without exerting any influence on the surrounding protoplasm. In Elasmobranchs the nuclei of the disc are rounded and regular in form, while those in the yolk are irregular in shape, and provided with knob-like processes. The cone-like nuclei are only found in the earlier stages, and they possess no distinct membrane.

Oellacher, who refers more especially to the nuclear zone as described by Kupffer, says there is no need to resort to free-cell formation, inasmuch as its protoplasm is the same as the rest of the archiblast, hence, in each, the segmentation-process is the same. Bambeke ingeniously suggests that an endogenously-formed yolk-nucleus may give origin to these nuclei, and that the cells of which they are the centres are segmented more slowly than the cells of the disc (No. 20*a*, p. 4); but, as previously noted,

* The failure to observe "direct" division will not, of course, appear strange to those who accept karyokinesis or indirect division as the sole process of nuclear multiplication, but all visible forms of division are here included.

† Lankester is also of opinion that the cells of the perimorula in *Gammarus locusta* arise as isolated structures like the autoplasts of Cephalopods (No. 92, p. 63).

neither a primary nor a later endogenously-formed yolk-nucleus has been made out in the vitellus of the Teleostei. Upon this vexed question centres the interpretation of the trophic part of the ovum.

That the periblast-nuclei are really autoplastic, would seem to be the conclusion most agreeable to the facts of the case,* and if the yolk were ancestrally divided into separate nucleated masses or cells, as was most probably the case, then upon the breaking down of these yolk-segments, to form the existing syncytium of the Teleostean ovum, the nuclear matter would likewise become diffuse. It is possible, therefore, to look upon the periblastic nuclei as the revival (segregation) of the primary nuclear bodies. The vitellus in one species (*Temnodon saltator*), described by Agassiz and Whitman (No. 2, p. 14), still shows the division into large yolk-segments without nuclei, though the segmentation is not total, a large central mass remaining uncleft. These large segments are much flattened, and appear beneath the marginal periblast, with which, during epiboly, they progress round the central yolk-nodule towards the vegetal pole. A similar condition occurs in the pelagic egg of the sole (Pl. XXII. fig. 1), in which a series of vesicles or segments appear under the disc in the lenticular stage, and spread with the blastoderm so as to form a superficial layer over the entire yolk. In the extremely pellucid egg of the sprat, again, the whole yolk is imperfectly divided into a series of polyhedral masses.

Even holding to the position that the cell is essentially of a uninuclear character, no difficulty is presented by the multinucleate periblast, for each may be regarded as the centre of a cell whose outline is undefined. It must be granted also that little difficulty is presented to those who regard the yolk as a single cell—if, as Butschli holds, a single cell during proliferation may exhibit all the gradations from a uninuclear to a multinuclear condition, and from the latter retrogress to the former condition without once forfeiting its character as a single cell. On the other hand, the syncytium, as Haeckel conceives it, though formed of cells originally separate, and including therefore many nuclei, is still a cell.

There are many appearances in the living ovum which indicate that the periblast contributes cells to the blastoderm, such cells being segmented extra-embryonically.† This point belongs to a later stage of development, and we can here merely make a reference to this segmentation of the periblast in its bearing upon the real significance of this layer.

In an ovum of *Gadus æglefinus*, at the close of the first day after fertilisation, the nuclear zone was well marked, and the homogeneous protoplasm composing it rose into minute prominences or depressed conical papillæ, upon each of which a nucleus appeared to be seated (Pl. II. figs. 4 and 4*a*, *n*). This botryoidal appearance was unmistakable,

* It would not be accurate to speak of these nuclei as genuine "autoplasts," for these latter bodies never become the centres of cells produced by cleavage. It is essential to the autoplast that the surrounding matrix remains unsegmented.

† The growth of the blastoderm by marginal conversion of cells is a phenomenon that continued investigation shows to be widespread; it occurs in many Invertebrates—in Cyclostomes, and, as Balfour and Deighton unmistakably demonstrated, in Birds. *Vide* "Renewed Study of the Germinal Layers of the Chick" (*Quart. Jour. Micr. Sci.*, xxii. p. 177).

and due, there can be no doubt, to planes of cleavage passing as linear depressions from the margin of the disc outwards. No cells could actually be seen to be completely segmented and added to the margin of the disc, nor could this be ascertained by study of the living ovum, for such cells transferred into the germ would enter the lowest stratum of the disc, and would therefore pass beneath the margin along the basal region—this margino-basal portion of the blastoderm being especially unfavourable for study in the living condition. There is no evidence against Brook's view, that matter passes into the archiblast in the early stages, and thus nourishes it—a view similar to that of Hoffman (No. 68), viz., that the nucleated periblast performs the function of provisional blood.

VII. Embryonic Shield and Rim.

We have traced the development of the ovum up to the stage which immediately precedes the formation of a distinct embryonic trunk, coincident with the radial thickening of the blastoderm. No clear differentiation into layers can as yet be made out, though the upper stratum is usually distinguished as a layer of ectoderm (Oellacher's "hornblatt") or epiblast (Pl. II. figs. 1–3, 6, and 15, *ep*)—the cells below, which form the main mass of the germ, being endodermal or lower layer cells (*ll*). This saucer-shaped blastoderm (Pl. II. fig. 19), consisting of two germinal leaves or layers, arches over the germinal cavity, while peripherally it is in contact with the cortical protoplasm of the yolk, chiefly that part of the cortex distinguished as periblast. Then commences epiboly, that remarkable process which Rathke, in 1832 (No. 129), was the first to describe in Teleosteans. The germinal matter which originally clothed the vitelline globe as a film, and afterwards becomes segregated at the animal pole, is now seen apparently retrogressing, and again encloses the yolk, not as a homogeneous envelope, however, but as a segmented cellular blastoderm. With the commencement of the process the blastoderm flattens (Pl. II. fig. 15, *bdm*), and the vertical height of the germinal cavity (*gc*) is by this depression so much reduced as to form a mere fissure, though otherwise its relations remain unaltered. On the second or third day, in the Gadoids and other forms here referred to, this flattening is clearly shown; and Lereboullet, who describes it in *Esox*, says that during the first half of the second day the blastodermic vesicle (*i.e.*, the germ) flattens more and more, its two opposing walls touch,* and it becomes moulded as a serous envelope round that part of the egg which it covers like a watch-glass (No. 93, p. 488). By this process of flattening and extension meridionally over the yolk-ball, the germ becomes distinctly thinner. This decrease in thickness is especially noticeable, Lereboullet says, in *Salmo fario* as compared with *Perca*, and epibolic extension in the trout is much less rapid than in the latter. Variations, too, occur in pelagic ova, but these are doubtless caused

* If our interpretation of Lereboullet be correct, it is not accurate to speak of the two layers, viz., the thin germ and the periblast, as really touching, though the interspace becomes less and less.

in a large measure by differences of temperature, light, the condition of the water, and other features of the laboratory, though the divergence between a pelagic and a demersal ovum in this respect is so marked as not to be fully explained in that way. Thus in *Gastrosteus* a blastoderm, which covered fully one-eighth of the yolk, had embraced in twenty-four hours only slightly over a quadrant, while in *Pleuronectes* it had extended over nine-tenths of the yolk-surface. Again, in *Gadus æglefinus*, when the temperature of the tanks was kept lower, epiboly was as slow as in the case of *Gastrosteus* under a higher temperature. When the germ covers barely a quadrant the margin becomes visibly thickened, this being the first indication of the embryonic rim (KUPFFER'S Keimsaum, OELLACHER'S Keimwulst), which plays so important a part in the formation of the embryo (Pl. II. fig. 17, *br*). This appearance of the rim LEREBOULLET connects with the thinning out of the germ, and explains it as a process of mechanical transference—the central cells passing to the circumference, as indicated by the increased density of the latter, which forms "a true pad around the egg" (No. 93, p. 458). The cells of the germ undoubtedly become greatly flattened, as we see in Pl. II. fig. 3, as compared with fig. 17, when extension has proceeded largely; but such a transmission of cells less truly represents the process of peripheral thickening than the inflection of old, the reception of new cells described below, and the aggregation of these in a marginal band.

We have referred to epiboly as to all appearance a retrogression,* but it is not really so, it is rather a process of invagination such as we find so widespread in the development of animal germs. This process, had the amount of food-yolk present allowed, would have resulted in the establishment of an involuted epithelial lining to the gastrula. The exaggeration of the trophic mass, which must ancestrally have been even much greater, prevents this progress of the ectoderm, and as its extension is not arrested, it follows that the yolk-globe is epibolically enveloped. While, as indicated, the germ becomes thinner, yet along one radius this decrease is not so great as elsewhere; in other words, the germ, soon after the close of segmentation, shows a thickened embryonic radius which never disappears (Pl. II. figs. 15 and 17). When the germinal cavity (*gc*) is formed, this portion is well marked, as the cavity lies in front of it, *i.e.*, eccentrically, and all through development it is thus distinguished by its greater thickness, so that LEREBOULLET cannot be correct in saying that the embryonic radius only commences when epiboly is nearly complete (No. 93, pp. 495–6). He failed, indeed, to notice in his species any trace of the rim until the blastopore is in its final stage, then, he says, a very distinct rim is formed around the "trou vitellaire" of VOGT. In the trout, as OELLACHER shows (see No. 114, Taf. i. figs. 2–5), this radius is well marked; but in other forms it is less apparent at an early stage, though the (embryonic) radius in all Teleostean ova is probably distinguishable from the non-radial portion by its greater thickness. In sections through the blastoderm before the equator is reached (Pl. II. fig. 17, and Pl. IV. fig. 8), the germ consists merely of two layers—ectoderm (*ep*)

* *Vide* E. E. PRINCE, *Annals Nat. Hist.*, July 1887.

and entoderm (*hy*), the cells of both being very much flattened; but along the embryonic axis several layers are present, and the cells are, in the living germ, more rounded and fuller than elsewhere. Similar larger cells also occur at the margin (Pl. IV. figs. 5*f*, and 7), and to the presence of these, as well as their closer arrangement, no less than the greater number of cells, is due the thickened appearance of the marginal belt or rim (*br*). It is clear that the blastoderm covers a very large superficial area, when compared with its extent at the close of segmentation, and this extension is largely, as we have hinted, a process of "flattening out" undergone by the originally rounded or polygonal cells of the archiblast. The cells are thus expanded superficially; but doubtless there is also a marginal addition of cells—periblastic in origin.

Beneath the rim and embryonic axis a single layer of cells intervenes, separating the germ from the yolk. This layer is, in fact, the third primary layer or hypoblast (Darmdrusenblatt), and its mode of origin is a point of great interest. How does it arise? The answer to this question is by no means easy, but the view that it is invaginated, *i.e.*, an inflection of the epidermal layer, is grounded upon appearances in the living ovum, and prepared sections (Pl. II. figs. 15, 17, *hy*) no less than upon phylogenetic considerations. A folding-in of the epiblast is indeed seen at a very early stage, but, when the germ has thinned out, this involution is more apparent (Pl. II. figs. 10, 17), and the centripetal advance of the rim can be readily followed by continuous watching, for, starting as a narrow peripheral band very slightly denser than the rest of the blastoderm, it advances slowly towards the central point of the animal pole. This region, known as the embryonic scutum (Oellacher's Embryonalschild), coincides with the embryonic radial thickening, which, as already noticed, is present from a very early stage. Lereboullet calls it the "bandelette primitive" or "germe embryonnaire," as being in his view the first indication of the embryo (No. 94, p. 255), but this is not so, the thickened radius preceding by an interval of many hours the inflection of the hypoblast, and being already distinguishable, when the germinal cavity appears. At first the scutum is a mere tubercle in the Salmonoids, as Lereboullet says, though flatter and more tongue-like in Gadoids, which pushes out from the rim and progresses towards the pole opposite to the blastopore. As it advances and extends laterally, it brings visibly into prominence the embryonic thickening, which, however, already exists, and when the blastoderm covers about one-fifth of the vitellus, this hypoblastic layer spreads out as a scutiform film or membrane beneath the embryo. That this process is one of true invagination is disputed. Götte, Henneguy, Cunningham, Kingsley, Conn, and others hold that it is so; whereas Oellacher regards it merely as a delamination, a simple differentiation *in situ* of the deepest layer of the primary entoderm, and this view Ryder and others adopt. Kupffer, Van Bambeke, His, Klein, and G. Brook regard the sub-blastodermic protoplasm or periblast as the source of this layer. Lereboullet speaks of it as a vegetation or proliferation (No. 94, p. 253), though he also seems to resort to a kind of mechanical transference of cells (No. 93, p. 488). We know that in Elasmobranchs this layer is formed partly by conversion of lower layer cells

in situ, and partly by invagination; in Cyclostomes and Amphibians it is in all likelihood invagination purely, and the prevailing view, that Teleosteans illustrate this latter process also, is probably true. In a section of an early blastoderm (Pl. II. fig. 15, *a*) the infolding has apparently begun at one point, but the cells of the single stratum—becoming crowded together—lie over each other so as to produce a multi-layered appearance (*hyp*). The layer inflected is, however, the outer or corneous layer, as GÖTTE holds, and this point is of some importance, for many authorities who favour the invagination-theory, differ as to the layer that undergoes inflection. Thus HENNEGUY, AGASSIZ, WHITMAN, and others, though holding strongly to invagination, declare that the outer layer is not concerned in the process—a linear fissure, it is maintained, wholly separating the lower or sensory epiblast from the outermost layer, the latter indeed ceasing at a certain distance from the margin. That the outer or corneous layer alone is inflected is the view of KINGSLEY and CONN (No. 78, p. 201) and others. Teleostean blastoderms are particularly unfavourable for deciding critical points such as this, the cells of the various layers being almost destitute of those peculiar distinctive features shown in many other groups, and an element of uncertainty must necessarily be connected with such a point as this. So far as HENNEGUY's view (No. 64, pp. 402–3) depends upon observations on the living ovum, it cannot be relied on, for this point must be determined by sections. If OELLACHER's well-known figures be referred to, we find in very early blastoderms that not only is the epiblast shown extending quite up to the periphery, but the flattened cells pass beyond the limits on to the surface of the yolk (No. 114, *cf.* figs. 4, 5, 6, Taf. i.); but such an extension beyond the margin of the blastoderm does not take place in the ova dealt with here, though the limits of the germ in section are difficult to distinguish, save in such a section as Pl. II. fig. 15, *a*.

In the living egg a fissure certainly can be distinctly made out, but it apparently ceases before the margin is reached. Optical considerations, again, would favour this. HENNEGUY, however, also urges that even in sections this point may be wrongly interpreted, as chromic acid preparations show the same appearance as that we have just referred to, and the obliteration of the fissure he attributes to the reagent. The view has been suggested (No. 122, p. 449), that while the process is one of invagination, it is more than that, since it embraces also a species of budding, such as LEREBOULLET alludes to (No. 94, p. 253), cells segmented from the periblast being added to the blastodermic margin, and folded in along with ectodermal cells. This vegetation of periblastic cells will probably be most active along the posterior edge of the scutum, but no evidence of this is indicated until a later stage. The entire rim is thus a region where peculiarly complex processes are going on, for not only is the outer edge continuously progressing towards the vegetal pole, but the inner edge is also advancing towards the opposite pole, and this is rendered possible by the combined inflection of epiblast-cells, and the inclusion of periblast-elements. It appears that KINGSLEY and CONN, while holding that the epiblast is really inflected as stated above, also regard the intermediary layer as adding cells to the invaginated hypoblast (No. 78, p. 209). The inflected cells creep up

as a single layer, except at the margin where they are heaped together (Pl. II. fig. 10),* are very much flattened towards the animal pole, and merge with the cells from other parts of the rim. The effect of this union (especially where the cells from the rest of the rim meet the cells of the scutum as it proceeds towards the same pole, as well as laterally) is, that the original very definite outline of the shield becomes irregular, and finally almost wholly disappears. The rim, however, does not vanish with the appearance of the carina, as KUPFFER and VAN BAMBEKE hold, nor are the two structures really so intimately connected as is often supposed. The rim continues even after the alar expansion of the scutum, for the reason just stated, is no longer visible. The shield, in fact, exists before invagination of the hypoblast, if by the shield be really meant the embryonic thickening, and not merely a *visible* scutiform appearance; but it passes insensibly away on all sides, save posteriorly. The invagination-cells do not so much produce the shield or carina as make both optically visible.†

The ectodermal and periblastic cells, which are inflected, result in the establishment of a single layer of flattened cells—a sheet, in fact, of continuous hypoblast, which, as HAECKEL held (No. 63, p. 91), limits ventrally the embryonic lamella. It separates the carina from the yolk, save in the caudal region, where sections even more than the study of the living ovum indicate the special activity which centres there. It is noteworthy that the rim does not contain any mesoblastic cells, as in *Rana*, the Teleostean resembling the Cyclostome (*Petromyzon*) in this feature. In the region of the scutum the hypoblast, of course, includes in its fold lower layer cells, but their significance at this time is indifferent. This view, we think, explains satisfactorily the origin of the primary rim, the thickening of the blastoderm, the extension of both, the definition of the embryonic scutum, and its subsequent gradual disappearance. At any rate, it is difficult to explain these phenomena by any process of delamination such as that of OELLACHER, RYDER, and others: differentiation *in situ* of the lowest stratum of the primary entoderm would hardly produce the definitely-bounded thickening, and the centripetal progress of the same. The whole appearance and behaviour of the cells of the rim in the very transparent blastoderms here considered, strongly suggests invagination rather than delamination. OELLACHER's figures (No. 114, Taf. i. and Taf. ii.), it is true, as strongly indicate delamination, though figs. 2 and 3, Taf. i. might represent an inflection of the lowest layer. At a later stage, when OELLACHER recognises a definite "unteres Keimblatt," the cells are rounder and larger than the superjacent cells, a condition quite the reverse of that which obtains in the Gadoids. It would appear as if the character of the constituent cells of the hypoblast in these groups were not only thus unlike, but that in its mode of origin very marked differences also existed. Mr

* This centripetal passage of cells, there can be little doubt, is of profound ancestral significance; it can be no less than "a real survival of the hypoblast cells to grow inwards during the process of involution" (BALFOUR, *loc. cit.*, p. 530).

† The curious notions of OELLACHER (*vide* No. 113, pp. 21, 40) respecting the various shapes assumed by the scutum at different stages, do not seem to be borne out by study of Gadoid and other forms; and the opinion formerly expressed by one of us (No. 123), that the shield shows differences in outline, characteristic of different species, also needs modification.

Cunningham's suggestion may indeed precisely express the fact, when he hints that this layer may be produced in Salmonoids by delamination, and in the Gadoids and other forms by a centripetal process (No. 48).

In either case the final result is the establishment of a continuous layer of flattened cells, which extends underneath the blastoderm, and forms an alar expansion on each side of the trunk of the embryo. Agassiz and Whitman speak of it as three or four cells deep below the embryonic axis; but this is true only for a slightly later stage, after proliferation has commenced. A typical section of the Teleostean on the establishment of the hypoblast, *i.e.*, when the yolk is about half covered, shows (as in Pl. II. fig. 17) a single-layered corneous epiblast, *ep*, formed of fusiform or flattened cells, which roofs over a thick mass of cells for the most part derived from a second layer of epiblast, the sensory or neurodermal stratum, *ll*, and lastly, the single layer of cells composed of the invaginated hypoblast, *hy*. The more or less acuminate snout of the embryo often appears to dip into the hypoblast in front, or rather the hypoblast (*hy*) seems to creep up and overlap the anterior end of the embryonic carina, *car*. (Pl. III. figs. 5 and 6). Posteriorly the hypoblast does not exhibit the flattened or squamous character, but forms a small tract of full, conical or cubical cells, *hy* (Pl. IV. figs. 5*b* and 6). These cells, which are quite at the blastoporic termination of the embryo, arch over a horizontal cavity, and form indeed a superior enteric roof, constituting, as Cunningham strongly and ably urged, a plate of dorsal hypoblast, and giving origin, as will be shown, to the notochord. These two important points fall to be considered shortly.

The germinal area after completion of cleavage may be said to present three successive phases,—first, it is composed of archiblast cells (Pl. II. figs. 1 and 2) of fairly uniform size, polygonal, uninucleate as a rule, and formed of clear protoplasm free from yolk-spherules; secondly, an upper stratum becomes slightly flattened, and may be distinguished as ectoderm, *ep* (Pl. II. fig. 3), while the mass of unaltered cells below forms the "lower layer" or primitive entoderm, *ll*; thirdly, the ectoderm, though at first a single layer, subsequently exhibits three or four layers, and the outer stratum is the epidermal or corneous epiblast ("Hornblatt," Oellacher, "Umhüllungshaut," Reichert, "Deckschicht," Götte); while the under stratum, which always consists of more than one layer of rounded cells, is the sensory epiblast, *ll* (Sinnesblatt of Oellacher), and this latter layer by rapid proliferation forms the neurochordal carina, constituting the main mass of the embryonic thickening, which below is limited by the single hypoblastic stratum, *hyp*. These three stages are represented in Pl. II. figs. 2 and 3.

Epiblast.—Little can be added by way of special remark in regard to this layer. Certainly the late distinct differentiation of the epiblast in Teleosteans forms a point of contrast to the condition in Elasmobranchs and Amphibians; but Ryder's statement that the epiblast, with the other germ-layers, is only split off when the shield appears (No. 141, p. 494),* will not apply to the forms mainly treated of here, for the epiblast is

* Lereboullet also in his forms (*Perca* and *Esox*) made out his epidermoidal layer only when the equator was reached (No. 93, p. 493).

visible, and is inflected as the peripheral rim when barely one-tenth of the vitellus is covered, whereas fully a sixth is enveloped before the expansion of the shield is indicated. When it first appears the outer layer is distinguishable only by the slightly depressed appearance of its cells. It is a single layer, and is difficult to make out, as it does not present the regular disposition or columnar character of the ectoderm in other forms. The second stratum is well marked when the blastoderm extends over a quadrant, and, as already pointed out, its cells are not at all depressed, but are rounded or polygonal, and form several layers—indeed, they are distinctly marked off from the corneous layer. The existence of this layer has been disputed by HAECKEL in these words—"I do not consider the idea of a special nervous layer many embryologists separate from the cuticular sensory layer to be confirmed;" * and KUPFFER denies that this layer exists laterally, for he distinguishes the corneous stratum only, and indeed doubts the presence of a median sensory layer as such, the outer epiblast appearing to him to merge in the neurochordal mass below, as though it alone gave origin to it (*op. cit.*, p. 243).

Mesoblast.—The origin of the mesoblast is still a point affording matter for discussion, but the Teleostean blastoderm, it may be readily surmised, does not offer great facility for deciding the matter.† That it is not a primitive layer, but is derived from one of the primary layers, *i.e.*, ectoderm or endoderm, is beyond dispute.

LANKESTER seems to have been the first to suggest that, viewed phylogenetically, the mesoblast arose as a paired outgrowth of the entoderm, a fact which KOWALEWSKY had ascertained to be true for *Sagitta* (No. 85, p. 827).

In the Mollusca and Annelida we know that the mesoblast usually arises not as a single sheet, but as two distinct masses, just as in *Amphioxus* and many Craniates. Thus SCOTT and OSBORN found in *Triton* that the two bilateral masses were invaginated as such, and were never confluent in the middle line, the axial epiblast and hypoblast being only in contact along that line (No. 147, p. 455). SCOTT also affirms in *Petromyzon* that some mesoblast (dorsal) is invaginated with the cells of the mesenteron, while the cells of the ventral mesoblast are derived from the superficial cells of the yolk; but SHIPLEY's later investigations have demonstrated that in this form no mesoblast is invaginated, the two longitudinal bands being differentiated *in situ* (No. 149, p. 244). BALFOUR showed, and he is confirmed by HIS, that in Elasmobranchs the two bands arise in the manner just stated (No. 14, pp. 35–56); but in *Lepidosteus* BALFOUR and PARKER give no account of the origin of the mesoblast. In certain Teleosteans, HAECKEL describes a bilateral development (*Jenaische Zeit.*, Bd. ix.), while KOWALEWSKY says it originates from an invagination of the embryonic rim (No. 86). In speaking of the epiblast, it was indicated that our observations do not show such an inclusion of mesoblast by the reflected layer of the blastoporic lip; and unlike the condition in *Rana* and other forms, the infolded layer, *hyp* (Pl. II. fig. 15*a*), is in close apposition to the epiblast, *ep*, above. In the middle line

* "Gastræa Theorie," see *Quart. Jour. Micr. Sci.*, vol. xiv., note on p. 32.

† It need hardly be pointed out that in so familiar an ovum as that of *Rana*, the precise origin of the mesoblast is really undecided, and it is still to be settled whether the layer is derived from the "intermediary" mass of small cells, or from the endoderm by proliferation, as seems more probable.

of the embryonic thickening, the proliferated epiblast, *nc* (Pl. III. fig. 1), and the lower layer cells, of course, lie above the invaginated hypoblast, *hyp*. These lower layer cells probably become largely converted into mesoblast, though it is certain that the hypoblast also buds off some mesoblastic cells. W. Wolff has recently expressed a view similar to this, though he denies that the mesoblast (Mittelkeim) arises in any way from the endoderm. The cells which build up the mesoblast represent, he holds, the surplus of those blastomeres which are not used in forming the gastrula (No. 160, pp. 425–448). According to Kupffer, His, and Klein, the mesoblast results solely from the differentiation of the deeper germ-layer, while the hypoblast is stated to originate in the periblast (Klein's "parablast"). Götte speaks of it as formed from the invaginated layer, which gives origin in addition to the hypoblast. The fact would seem to be that much mesoblast is formed from the lower layer cells, *ll* (Pl. II. fig. 15), these cells being a continuous sheet, viz., the primary entoderm of the early two-layered blastoderm, and they become severed into two longitudinal masses, *mes* (Pl. III. figs. 2 and 11; also Pl. IV. figs. 5 and 10), by the proliferation of epiblast, *ep*, which produces the medullary plate, or neurochord, *nc*. The sub-ectodermic mass, *ll* (Pl. II. fig. 15), cannot be regarded as mesoblast until it is severed mesially—the mesoblast, when recognisable as such, is defined as two lateral plates, just as in *Petromyzon* (Calberla), *Triton* (Scott and Osborn), Elasmobranchs, and other forms. Kingsley and Conn speak of this continuous sheet, at an early stage, but their figures are not decisive. Thus their fig. 25, to which they specially refer, as also figs. 26 and 27, show a massive dorsal plate, which must be the thickened epiblast, *i.e.*, the neurochordal proliferation, and against it the notochord abuts below. The mesoblast must, in part, constitute the lateral plates, though the authors themselves do not so interpret their figures. This interpretation appears, in fact, irresistible, though it is not in agreement with the view stated in the text (No. 78, p. 200). Ryder* records a peculiar condition in *Elecate*, viz., a precocious metameric segmentation in the two parts of the rim which diverge from the posterior end of the trunk. This is very remarkable, for no such feature has been seen in any other form, while in those referred to in this paper, the posterior portion of the trunk, after the mesoblastic plates are defined anteriorly, shows no such differentiation, the three layers of the mid-region merging, in fact, in a mass of indifferent cells at the posterior termination (*vide—prs*, Pl. III. fig. 12, and Pl. IV. figs. 5*d* and 5*e*). These two mesoblastic plates, as seen in section *mes* (Pl. III. fig. 11), have above a thin covering of epiblast, *ep*, and inferiorly an insinuating layer of hypoblast, *hyp*, which separates the embryo from the yolk below. Anteriorly the mesoblast thins away, and in the otocystic region is reduced to a single layer of somewhat depressed cells, *mes*, between the hypoblast, *hy*, and the greatly enlarged neurochord, *mo* (Pl. IV. fig. 4). In Oellacher's figures of the trout at this stage, the mesoblast is not so much reduced; but its larger bulk is probably connected

* Ryder's view of the origin of the mesoblast is not clear; he apparently favours delamination with Oellacher (*op. cit.*, pp. 494–95), and hypoblastic proliferation (on p. 570); while on p. 501 he seems to suggest a sundering of the "lower layer" mass, such as is insisted upon above.

with the diminished neurochordal mass (*vide* No. 114, Taf. iii. figs. viii$_4$ and ix$_1$) in that form.

Further forward (Pl. IV. fig. 3) it apparently ceases altogether, the cells beneath the optic vesicles, *op*, being hypoblastic, while the denser stratum, *ep*, above, is neurodermal (sensory epiblast), unless the small strand of cells filling up the triangular fissure on each side be a continuation of the mesoblast behind (marked in the fig. *mes?*). Oellacher's representation of this region is not unlike our fig. 3, Pl. IV., but here again mesoblastic cells are shown as somewhat abundant; his mesoblastic "Kopfplatten" consisting of three or four layers, which continue laterally as flattened peritoneal plates. This latter structure is wholly absent in our forms, the marginal alæ being simply epiblast and hypoblast, though the very minute group of cells mentioned (*mes?* Pl. IV. fig. 3) may represent Oellacher's cephalic mesoblast. Our figures (Pl. IV. figs. 3, 4, 16, and 16*a*) support the view that the mesoblast does not yet extend into the head-region, the cells at *x* and *y* being obviously neurodermal. If the foregoing conclusion be correct, the mesoblast arises for the most part *in situ* from the lower-layer cells in the trunk-region proper—that is, excluding the pre-otocystic and caudal portions—by a process not of delamination purely, but of mechanical separation, the intruding neurochordal cells from above actually pushing aside the subjacent cells as two longitudinal lateral plates.

It is not easy to see why mesoblastic cells should, as appears to be the case, be absent so largely from the cephalic region. Their absence would be accounted for if the mesoblast be really a forward growth from the trunk-region, and most probably also from the posterior mass of indifferent cells. Such a forward growth has been regarded as the sole process of mesoblastic growth (Kölliker, No. 81); and if in its differentiation the mesoblastic cells are separated at first just in front of the primitive streak, it will be difficult to show that some such process of forward growth is not involved. The cells, in fact, below the primary ectoderm form a median layer, when the rim is first invaginated below it, and since Balfour and Deighton find in the chick (No. 19, p. 180) that the main mass of the posterior indifferent cells (primitive streak) is really produced by epiblastic proliferation, it follows that some mesoblast is really indirectly of epiblastic origin. Bambeke, indeed, regards the mesoblast in Teleosteans as the lowest delaminated stratum of the primary upper layer of the germ (Von Baer's animal layer), *i.e.*, ectoderm. This upper layer in his view divides into three, viz., the corneous, neurodermal, and mesodermal layers (No. 20*a*, pl. iii. fig. 8, pp. 57–58). Delamination solely will not account for the fact that in Teleosteans the mesoblast is certainly best developed in the posterior region,* as would be implied by the theory of forward growth, and we see that it thins away anteriorly. A comparison of figs. 3, 4, and 5*a*–5*c*, Pl. IV., sufficiently demonstrates this. Even at a later stage the same feature appears (see figs. 10 and 11, Pl. IV.), as though the mesoblast in extending anteriorly into the head receives continual additions from behind. In *Petromyzon*, Shipley, indeed, regards the muscular elements of the mouth

* This is also the condition in Elasmobranchs, the mesoblast being accumulated at the posterior end as prominent tail-buds (*loc. cit.*, p. 557).

and gills, besides the eyes and mouth themselves, as developed from wandering mesoblastic cells as well as unsegmented mesoblast (No. 150, p. 336), and these wandering cells WENCKEBACH has recently affirmed to be active in Teleosteans in building up the heart and its connected trunks, and other parts of the embryo (No. 158). It cannot be denied that in fig. 2, Pl. III. and figs. 4, 5*a*, and 5*b*, Pl. IV., the mesoblast has more intimate relation to the hypoblast than to the epiblast, and the condition presented by these early sections corroborates the view that the mesoblast is of hypoblastic origin, as GÖTTE strongly holds (No. 58). That the mesoblast in the Teleostei has in fact a threefold origin is consonant with the figures given in various plates,—part being formed directly by conversion of lower layer cells *in situ*, while part is proliferated from the invaginated hypoblast beneath, and lastly to make up for the forward growth of these cells into the cephalic region, other mesoblastic cells are derived from the indifferent mass constituting the caudal region. It is singular that this account of the multiplex growth of the mesoblast should coincide, even down to many details, with the derivation of this layer in the chick, according to BALFOUR and DEIGHTON. In their paper (No. 19) part of the mesoblast is determined to be from the indifferent cells of the primitive streak, primarily epiblastic (*Ibid.*, p. 182); some mesoblastic cells, which are stellate, are differentiated from the hypoblast (pp. 184–5); while certain others lying below the epiblast in the early blastoderm (see No. 11, fig. 91, *l*, p. 150), and really "lower layer" cells, BALFOUR considers "have also a share in forming the future mesoblast" (p. 154). KINGSLEY and CONN, though they furnish no account of the process, come to a similar conclusion, and hold that this middle layer is derived partly from hypoblast and partly from lower layer cells (No. 78, p. 200).

HYPOBLAST.—The hypoblast, *hy*, which there can be little doubt is pushed in from the periphery as an inflected layer of ectodermal, for the most part "corneous layer" cells, *ep*, with some cells derived from the periblast, *per*, insinuates itself between the under surface of the germ, *ll*, and the cortex of the yolk, *y*, forming the limiting layer on the ventral aspect of the embryo. It separates the neurochord (*ne*, Pl. IV. fig. 5*a*) in the middle line and the lateral cells, *mes*, destined to form, in part, the mesoblast, from the yolk, *y*. It remains for some time as a single layer of flattened cells, *hy*, in the anterior and mid portions of the embryo; but at the posterior termination (Pl. IV. figs. 5*d* and 6) its character alters, for it is there less definite, merging, in fact, with the heaped-up periblast, *per*, like the thickened layer of dubious cells, which in the chick continue into the "germinal wall" behind (No. 19, p. 179). This tract of mingled hypoblast and periblast is the site of much developmental activity, and about the time that the blastopore closes it becomes defined as a bridge of swollen columnar cells, *hy*, in the median line, arching over a fissure below, and pressing against the neurochord, *ne*, above (figs. 5*b* and 6, Pl. IV.). We see here the very phenomenon which KINGSLEY and CONN* and CUNNINGHAM have suggested, viz., that the invaginated hypoblast is really "dorsal hypoblast, roofing over a primitive enteric cavity, whose floor is

* *Op. cit.*, p. 201.

granular protoplasm with many nuclei, and cells apparently forming around them." Anteriorly, the hypoblast still preserves its flattened character (*hy*, Pl. IV. fig. 5*a*), while in the otocystic region it seems to merge in the neurochordal cells, *ne*, unless the undefined cells in the middle line be a thin stratum of mesoblast, in course of formation, and destined partially to constitute the nuchal and cephalic mesoblast (Pl. IV. fig. 4). A similar indefinite axial tract occurs in the chick (No. 19, p. 184). Further forward the hypoblast is once more fairly defined (Pl. IV. fig. 2), and at the tip of the snout, as before mentioned, it may often be distinctly seen to overlap the epiblast as a thin veil (figs. 4–6 and 19, Pl. III.).

The Blastopore.—The blastopore (Dotterloch—trou vitellaire) may be said to exist from the moment that epiboly begins. It coincides with the margin of the germ, and forms in fact the border of the saucer-like blastoderm at the conclusion of cleavage. Later, however, it is more distinctly recognisable as a kind of spacious mouth, from which the ball of yolk is seen projecting. Small granules often occur plentifully at the margin of the rim, and are imbedded in the periblastic ring (Pl. III. fig. 16). The continued extension of the germ over the yolk produces certain changes, notably in its diameter, which are easily observed.

Contrary to Oellacher's view, the rim seems to progress at an equal pace at all points, and it thus increases in diameter until the process of enclosure is half accomplished; but after the equator is passed, the aperture necessarily diminishes, and finally presents a fairly circular form. Oellacher regards the caudal end of the embryo as a fixed point, so that the parts of the rim further away from this point advance at an increased rate—progress being, in fact, rapid in proportion to their remoteness (No. 114, p. 4). This assumption, however, is very questionable, the snout of the embryo being apparently the fixed point, while increase in length takes place in the caudal region. No part of the rim can be shown to be stationary, for the embryo lengthens as epiboly proceeds, and no part presents more signs of active growth and development than the posterior extremity, as already indicated.

The lip of the invaginated rim, for which the name blastopore is on every ground justifiable, attains its maximum size when the equator is reached, and after that stage it continues to diminish until finally it closes. Often it assumes an oval form (*bp*, Pl. III. figs. 7, 23 ; and Pl. XXVIII. fig. 5), doubtless due to the plastic nature of the yolk; but usually an almost perfectly circular outline is preserved. In some cases the blastopore has the rude outline of a flask, the narrow portion forming a bay, which coincides with the caudal end of the embryo, and this has suggested the theory of concrescence in these forms. In most cases no such terminal bay is seen, the embryo in fact projecting more or less prominently, and breaking the circular outline of the blastopore in a manner exactly the reverse of that just mentioned. In the later stages of development *in ovo* the concrescence theory is not clearly borne out, *e.g.*, by the view of the gurnard (Pl. XIV. fig. 7), in which the rim forms a backward loop at the tail. This concrescence, however, may occur without a visible bay or angle directed forward, as indicated by

J. T. Cunningham. Again, it is observed that towards the closure of the blastopore the "limbs" of the blastoderm seem to go—so far—into the embryo. When this projection is less marked the caudal end of the embryo may still destroy the regularity of the circumference, as in Pl. III. fig. 23, recalling the horse-shoe-shaped blastopore of *Astacus*, such variations being easily explained by the bulk of the contained deutoplasmic matrix and the tension of the blastodermic membrane. This pressure outwards, as Van Bambeke pointed out, and the restraint of the blastoderm, frequently produce a contracted opening, like the mouth of a balloon (see Van Bambeke's figure, No. 20*a*, pl. ii. fig. 9), from which a plug of yolk protrudes, just as in the Crustacean ovum, mentioned above, an endodermal protrusion fills up the blastopore. In Teleosteans, as in *Astacus*, the plug diminishes as the blastopore closes. In the gurnard, as the blastopore closes, projecting cells are seen, which often send out protoplasmic processes, those protruding from the blastoporic lip somewhat resembling the processes which under pressure are pushed out from the marginal cells of the blastodermic ring at an earlier stage (Pl. II. fig. 16). The time of the closure of the blastopore of course varies, according to circumstances, in common with the other features of development. Thus in *Trigla gurnardus* the closure was observed to be effected on the third day after fertilisation; whereas in another series earlier in the same season (May), the temperature being lower, this did not occur until the fifth day. As closure takes place the yolk may often, in side views, be seen still to project as a diminished yolk-plug (Pl. III. fig. 15); but usually as closure is effected the blastopore forms a trumpet-shaped opening, round which the deeply corrugated lip rises as a circular eminence (Pl. III. figs. 9, 10, 21).

Kupffer's Vesicle.—When the blastopore closes, or often a few hours earlier,* a minute vesicle arises on the ventral aspect of the embryo slightly anterior to the caudal termination. Its advent is preceded by the appearance, in some cases, of vesicles or small elongated spaces (Pl. III. fig. 17), evidently filled with colourless or pinkish fluid. They occur quite at the margin, as if the advancing embryonic area became elevated at these points, and progressed over them. In other cases a granular thickening occurs in which a few rounded vesicles are imbedded, as can be readily seen in *Trigla gurnardus* and other forms shortly before the blastopore closes. Kingsley and Conn noted such a group of minute vesicles, which in five hours apparently by coalescence showed the characteristic form and appearance of Kupffer's vesicle. It is defined in their figure, above by hypoblast, and below by periblast (No. 78, pl. xvi. fig. 54). It is variable in the precise time of its appearance, for Henneguy noticed it in *Salmo fario* when only about half of the vitellus was covered by the blastoderm (No. 80). In *Molva vulgaris*, *Gadus morrhua*, and other species it is usually not visible during the open state of the blastopore, but both in position and time of its appearance it varies, though the clear vesicular structures, with a delicate envelope, are usually exhibited. Kupffer, who first described it in *Gastrosteus*, *Gobius*, and others, calls it the "allantois," and says that it acquires a coating of cylindrical epithelium, and finally becomes the bladder, though he did not show how the

* J. T. Cunningham found that in *Clupea* it was late in appearing (January 1886).

primary "Urnierengange" communicated with it (No. 88). Henneguy also speaks of a cellular wall, but it appears to be more truly a wall of clear protoplasm in which nuclei rapidly develop, and not wholly a wall of cylindrical cells. In regard to form, it may be more or less spherical (*kv*, Pl. XXIII. figs. 8, 9), or markedly ellipsoidal (Pl. XXII. fig. 12), this latter figure being frequently altered by the flattening of its floor (*kv*, Pl. III. figs. 21, 22) and the increased curvature of the roof,—changes best seen in side views; while again its shape may be wholly irregular (Pl. III. fig. 14); or lastly, it may simply take the form of a sub-embryonic fissure. Secondary vesicles are very frequent, and they present the same features as the normal vesicle (Pl. XXIII. fig. 9); but may extend all along the ventral line almost to the pectoral region. In the gurnard this multiplicity of vesicles is often a very striking feature, whether extending along the sub-alimentary region, or accumulated together as a prominent cluster of bubble-like structures. A small anterior vesicle in addition to the normal one is often seen (Pl. III. fig. 20, and Pl. XXIII. fig. 8), and a connecting granular strand, but there is no apparent tendency to amalgamate. The diameter of the larger vesicle in an example of *Gadus æglefinus* was found to be ·005 inch, but occasionally, as in *Trigla gurnardus* (third day), the vesicles which form a group may even be five or six times larger than the ordinary vesicle. An embryo of *G. æglefinus* was observed to exhibit one or two small vesicles near the large vesicle, and three hours later, the large or normal vesicle and one of the smaller were almost free from the embryo, being in fact pressed into the surface of the yolk. Other three vesicles had developed and occupied the region whence the large vesicle was protruded, and shortly after, on viewing from above, the vesicles were seen to be upon one side of the trunk, viz., that to which the tail was bent. Still more remarkable was the situation in some examples of *G. morrhua*, for just before the blastopore closed, in addition to the ordinary vesicle, a large clear vesicle also occurred midway along the trunk, and it deeply indented the yolk. Moreover, a vesicle also appeared at the tip of certain protoplasmic pseudopodia which were pushed out from beneath the embryonic trunk. In another example, Kupffer's vesicle was situated posterior to the caudal termination upon a process of protoplasm. Agassiz and Whitman called attention to appearances similar to the foregoing (No. 2, p. 73), designating them "secondary caudal vesicles," and observing that they differed little if at all from Kupffer's vesicle. Whatever significance be attributed to this latter structure, it is in any case simply a fissure or cavity beneath the embryo (see section *kv*, Pl. IV. fig. 5*b*), and is defined usually by the dorsal hypoblast, *hy*, above, and the periblastic matrix, *per*, below. Its contents are usually homogeneous and clear, evidently a translucent plasma, though occasionally granules find their way from the basal portion of the vesicle into its lumen. Such being its structure, it is not remarkable that it should vary in shape, or often be a compound instead of a single vesicle. Balfour (No. 11, p. 61), Rauber (No. 133), and Balbiani (No. 9) favour the view that it is of ancestral value, and represents the invaginated enteric cavity of Cyclostomes and Amphibians.* Henneguy could not make out any

* See also a discussion on the subject by J. T. Cunningham (*Quart. Jour. Micr. Sci.*, January 1885).

canal connecting it with the exterior, either in transverse or longitudinal sections; but sections cannot satisfactorily demonstrate this point, the vesicle itself being evanescent, and its walls of delicate protoplasm are so readily affected by reagents, that a minute fissure is easily reduced or closed, so as to be indistinguishable. Study of the living condition is therefore most reliable upon this point, and it must be observed that Henneguy did make out a canal connecting the vitellus with the dorsal surface of the embryo; but he regards it as wholly independent of Kupffer's vesicle, for this latter structure, he says, has disappeared some time before. But in so delicate and transitory a structure as this vesicle, it is important only that its *site* should be regarded, and there can be no question that such a posterior canal passing to the yolk beneath the embryo is in communication with that site, even though the vesicle itself be no longer distinguishable. The enteric cavity at this stage is little more than a fissure between the (dorsal) hypoblast and the yolk-cortex or periblast; and Henneguy's canal can be no other than the post-anal passage trending round from the dorsal groove to the under surface of the embryo (that is, the surface of the yolk in Henneguy's view), and connecting the transitory medullary groove, with the no less transitory primitive enteron known as Kupffer's vesicle. Ryder admits that a neurenteric canal is represented, but not by a tubular connection; the solid caudal mass, where hind gut and neurula mingle, must, he holds, in its axial part, represent the canal. But Ryder also noticed a fine canal passing from the vesicle to the blastopore, and says—"I reserve my decision as to its true nature" (No. 141, p. 527).

Neurenteric Canal.—As the blastopore closes, a favourable side view of the caudal region shows a faintly marked fissure (*nec*, Pl. III. figs. 9, 20, and 22), or rather what seems to be a tubular connection of the external blastopore and the ventral surface of the embryo. Unless the chamber *x* (Pl. IV. fig. 5*d*), be an artificial product, the tubular character is demonstrated in the section. This slight cavity curves downward from the blastopore, and widens out laterally beneath the embryo (Pl. III. figs. 8 and 8*b*), passing for a short distance forward as a mere line marked by fine granules, and disappearing, as Kupffer's vesicle, or the site of it, is reached. Any actual union of the two vacuolated spaces is not easily made out, but the merging of the tract just described and the protoplasmic wall of Kupffer's vesicle is unquestionable (Pl. III. figs. 20 and 22). In fig. 9, Pl. III., the course of the canal, *nec*, from the corrugated blastopore, *bp*, forward is well seen, but Kupffer's vesicle is not yet defined; and the relation of the two is better seen in figs. 20 and 21, above mentioned, where the vesicle, *kv*, a minute lozenge-shaped chamber, is undoubtedly related to the tract, *nec*, posterior to it. Certainly the passage, *nec*, in fig. 22, is most readily, and without doubt correctly, interpreted as a neurenteric canal.

The existence of such a canal in Teleosteans has often been questioned, and, indeed, Miss Johnson amongst others declares that no such structure is known in these fishes, nor an invagination giving rise to a blastopore (No. 76, p. 666); though Kowalewsky is stated to have announced in an early volume of the *Arch. f. Mikr. Anat.* (vol. vii. p. 114) such a connection of the alimentary tract with the dorsal groove in Teleostei; and

Kingsley and Conn refer very briefly to what they style a "neurenteric canal," of which they give a figure (No. 78, fig. 30, pl. xv.). Raffaele also recently alluded to it in *Uranoscopus* (*op. cit.*, p. 28). That it has been rarely observed, and never fully described, is probably due to its evanescent character, and it may in some cases, indeed, never be developed. Balfour and Deighton (No. 19, p. 185) speak of it as "that most variable structure in the chick," and the same description may be applied to it in the Teleostean ovum. This canal can hardly be due to the supposed process of concrescence, as it has not the character so much of a vertical fissure as a depressed cavity passing obliquely downward and forward between the embryo and the yolk, and is best seen in transverse or side view. It is, indeed, less of a tubular canal than of a tranverse fissure between the convex embryonic surface and the concave yolk-surface, and opening externally by the blastopore. In Pl. III. fig. 8, in the living condition its course is clearly indicated, the shallow dorsal groove continuous with the blastopore indenting the caudal region, and then merging in the descending tract, *nec*, which widens out and becomes lost in the mass of periblastic protoplasm, *kv*, in which Kupffer's vesicle makes its appearance. Sometimes this neurenteric passage connecting the neurochordal groove above and the enteric region below is a distinct interspace (Pl. III. fig. 9, and possibly *nec?* Pl. IV. fig. 5*d*). It is often marked by granules (Pl. III. fig. 22), or even a tract of undifferentiated protoplasm, in which two or three clear spheres are imbedded (Pl. III. fig. 20). Fig. 8, Pl. III., for instance, showed this last named condition at 10 A.M., with a connecting tract opening externally between the closing lips of the blastopore. An hour and a half later, a spindle-shaped plug (Pl. III. fig. 8*a*) sending outward an acuminate process, interrupted the canal, *nec*, and presented amœboid movements. The plug then coalesced with the margin of the blastopore, and, assuming a distinctly granular appearance, formed a bridge across the fissure connected with the inferior tract (fig. 8*c*).* Meanwhile, the clear vesicles mentioned above had enlarged, and finally coalesced to form Kupffer's well-known structure. Such a plug as we have described Balfour and Deighton noted in the chick, and they speak of a mass of rounded cells pushed up through the neurenteric canal (No. 19, p. 186). The phenomenon just detailed shows two important points, viz., the connection of the external blastoporic orifice with the region of Kupffer's vesicle, if not with the actual structure itself, and the obliteration of the passage of connection, *i.e.*, the neurenteric canal, by a plug probably pushed up from below.

The section figured in Pl. IV. fig. 5*d*, and already referred to, passes through the precise region we have been dwelling upon, and a few loose cells alone obstruct the connection of the dorsal and ventral (enteric) groove, *ne*. The section is interesting as showing a portion of Kupffer's vesicle, or the groove itself imbedded in a thick layer of periblast, *per*, as we have before described.

Now the sections figured (Pl. IV. figs. 5*b*–5*d*, and fig. 6) clearly show the continuity

* Fig. 8*b* is an intervening stage, when neither plug nor connecting bridge are visible.

of the enteron formed by an arch of columnar hypoblast, *hy*, and a floor of nucleated (periblastic) protoplasm, *per*, the ill-defined ascending interspace or canal, *nec*, being bordered by indifferent cells, and opening by means of the blastopore into the dorsal groove above. This dorsal groove is more fully treated of on another page, and it can be no other structure than the primitive involution forming the medullary canal in so many forms, but in Teleosteans simply appearing as a transient, ancestral reminiscence, and, except for this, now obliterated. Certainly its connection with the subsequent permanent neural cavity cannot be demonstrated.

So rapidly does the dorsal groove become effaced that in a large series of sections of early stages none indicate this structure favourably; but a reference to OELLACHER's well-known figures (No. 114) sufficiently shows this, the deep groove in fig. iv. 3, Taf. ii., being merely indicated in fig. vii. 5, Taf. iii.; while the figs. in Taf. iv., such as fig. iv. 1, show no trace of it, nor can the permanent cavity be said to be more than foreshadowed. Owing to the rapid and complete obliteration of the medullary groove, the absence of a post-anal canal has been generally accepted for Teleosteans, and for this reason BALFOUR, though adding a query to his cautious statement, concluded that no neurenteric passage was "apparently developed" (No. 10, p. 286). BALFOUR and PARKER (*Phil. Trans.*, 1885, ii. p. 365) speak of the neural canal arising in *Lepidosteus* as a slit-like lumen, and not due, as supposed by OELLACHER for Teleostei, to an actual absorption of cells. "When first formed, it is a very imperfectly defined cavity, and a few cells may be seen passing right across from one side of it to the other" (fifth day after impregnation). The connection in Teleosteans between the primitive enteron, no other than the gastrula-cavity (see page 713), and the primitive dorsal groove cannot be questioned if our interpretation of figs. 9, 21, and 22, Pl. III., be correct, for the continuity of this groove, *nec*, and the blastopore, *bp*, is very apparent. The formation of a neural canal by a dehiscence of neurochordal cells is a secondary process, and the Teleostei therefore form no exception to the condition which so widely obtains in other Vertebrata, and which was demonstrated by GASSER in birds, by KOWALEWSKY, BALFOUR, HIS, and others in Elasmobranchs, by OWSJANNIKOW in Cyclostomes, and by GÖTTE and others in Amphibians.

Medullary Groove.—The permanent neural canal is formed comparatively late in osseous fishes, whereas in most vertebrates its appearance as a groove on the dorsum is a very early feature in development. For a short period, soon after the optic vesicles are defined, a transient longitudinal indentation passes along the median dorsal line from the head to the tail, just as LEREBOULLET figures (No. 95, pl. ii. fig. 36). It may be regarded as actually reaching to the lip of the blastopore, though the depression is so slight, in the extreme posterior region, that it is in some cases indistinguishable. In *Rana* at a certain stage the hind part of the neural groove cannot be made out. SPENCER, however (No. 151, p. 97), found that it extends quite to the caudal margin, but in this latter region it is obliterated—the cavity closes up, and the nervous cord becomes solid. The hind end of the trunk in the embryonic Teleostean often appears like a flattened plate, in which the neurochord spreads out like a spatula (Pl. III. fig. 16).

This flattened condition frequently continues for some time after the closure of the blastopore (Pl. III. figs. 18 and 20). It is merely a shallow groove, barely perceptible posteriorly, and does not therefore enclose the blastopore, which remains open for a short time, as a pore with a corrugated margin, but in the cephalic region the groove forms, as in the gurnard (*dg*, Pl. III. fig. 4), quite a deep fissure, showing itself earliest anteriorly, and extending, as VAN BAMBEKE describes, in the form of "a slight depression," the "sillon primitif" (see his fig. 12, pl. ii.), to the tail. In the forms here considered, the two lateral folds are by no means sharply ridged, and viewed from above the furrow is difficult to make out; and is thus unlike the condition in *Esox*, which LEREBOULLET says is distinctly marked by two parallel lines —the groove being deepest in the mid-trunk, and gradually disappearing before and behind (No. 95, p. 516). In the mid-trunk, he remarks, it likewise remains open for the longest time (p. 528). This groove is, however, as before suggested, merely a reminiscence of the ancestral condition, and wholly disappears chiefly by the horizontal widening out of the embryonic trunk as the blastoderm proceeds to envelop a larger extent of the vitelline globe.* This is evidently the case posteriorly, but in the head-region obliteration is achieved less by elevation of the base of the groove than by coalescence of its walls.

KUPFFER maintains that it is not by any means the homologue of the medullary groove of higher Vertebrates (No. 87, p. 251); while OELLACHER regards it as produced by the formation of the carina, the furrow deepening as the keel presses downward, and it is certainly true that the furrow is produced subsequent to the growth of the carina, and does not, as he proved, become the medullary canal; but the view adopted in these pages, that the carina is a neurodermal proliferation and the dorsal furrow an ancestral reminiscence, agrees best with appearances in life and in sections. Certainly no confirmation is given to CALBERLA'S opinion that ectodermal cells are involuted along the central dorsal line to form the epithelial lining of the neural canal, as the same authority, supported by W. B. SCOTT (No. 145), holds to be true for Petromyzon.†

As a matter of fact, the dorsal groove in Teleosteans does not appear to become any organ, but wholly passes away. It is subject to great variation, just as in the chick, for at times it is apparently entirely wanting, or at most is represented merely by a shallow depression, which may be discernible in the short posterior part of the indifferent caudal mass.‡ This posterior mass of indifferent cells, to which reference has frequently been made, forms the termination of the embryo (Pl. III. figs. 18, 20–22), where it reaches the lip of the blastopore, *bp*. In it neither neurochord, notochord, nor mesoblastic

* The superficial extent of the Teleostean embryo is a characteristic feature, and the dorsal groove is thus opened out on account of the large bulk of the yolk upon which the germ lies flattened. RYDER makes a passing reference to this (No. 141, p. 564).

† This epidermic involution in *Petromyzon* has now been disproved by the recent investigations of SHIPLEY (No. 150, p. 9).

‡ Compare the observations of BALFOUR and DEIGHTON on the chick (No. 19, p. 183).

plates can be distinguished, for all these melt into a common aggregation of cells, below which even the hypoblast, as BALFOUR and DEIGHTON note also in the chick (No. 19, p. 180), is hardly separable as a defined layer (Pl. III. figs. 3 and 12, and Pl. IV. figs. 5*b* and 5*c*). The epiblast (*ep*, Pl. IV. fig. 5*d*) laterally is partially differentiated; but in the middle line it merges in the cells below, to which, indeed, it gives origin. All these features point to its identity with the primitive streak of higher forms. The primitive streak, it is true, according to the accepted interpretation, arose in the process by which the embryonic trunk, notably in the Sauropsida, was removed from a marginal to a more central position on the surface of the yolk. This transference drew after the embryo, as it were, the diverging arms of the blastoporic lip, and their cells form a post-embryonal mass, which is the primitive streak. In *Rana temporaria*, as SPENCER found (No. 151, p. 97), the point where the medullary groove opens into the blastopore becomes solid, the neurochord losing its canal, and the epiblast, mesoblast, and hypoblast fusing as an indifferent mass just anterior to the blastopore. The Teleostean embryo reaches to the periphery of the blastodermic area, and any similar aggregation of indifferent cells is reduced to its smallest limit, yet such an aggregation exists, as a transient posterior mass, into which the notochord and other structures, anteriorly placed, pass and disappear. It is so in the chick, and in both the structure is transient—its importance goes with the earliest embryonic stages, and it disappears, or rather is used up, partially as we have seen, in the production of mesoblast, and still more by the extension posteriorly of the embryonic trunk, and the development of the tail. Its position on the anterior margin of the blastopore is easily explained, the present anterior margin is really the primitive posterior margin. If the blastopore extended to the ventral surface of the embryo, an increase in the amount of food-yolk would cause its true anterior margin to be pushed away from the ventral surface, and as it was thus carried outwards, the true posterior margin remaining unmoved, the parts of the blastopore would become reversed, just as a pendulum, if held horizontally in a north and south direction with the weight north, would with the first swing become reversed, the fixed attachment would point north, and the weight (*i.e.*, the true north end) would become south, and thus it is that the present posterior edge of the blastopore is really the former anterior margin. According to this view, we see that the blastopore, having drifted outwards, no longer coincides with a ventrally placed anus; and the relations of the primitive mesenteron, post-anal gut (Kupffer's vesicle), and neurenteric connection with the dorsal groove are placed in a clear light by means of the blastopore.

VIII. General Development of the Trunk.

After the closure of the blastopore, the definition of the embryo as a cylindrical rod, pressing somewhat deeply into the surface of the yolk (Pl. III. figs. 1–4), becomes marked. Anteriorly its enlarged cephalic region soon rises boldly above the surface of the periblast; while the trunk, though prominently standing out along the dorsum, and indenting the yolk in a pronounced manner ventrally, yet laterally, by the alar expansion of the scutum on each side, gradually merges in the general expanse of the blastodermic envelope, as observed in the serial sections (figs. 3, 4, 5*a*–5*d*, Pl. IV.). The true limits of the embryonic trunk are in reality not defined, the neurochord, *ne*, and myotomic masses, *mes*, are distinctly marked, but more distally, in the snout and tail, as well as the lateral regions, no sharp line of demarcation divides the young fish from the blastodermic area beyond. The embryonic Selachian or bird is pinched off more or less sharply at an early stage; but the Teleostean embryo, instead of becoming folded off as it were from the yolk, continues to lie extended upon its surface, and gradually draws the vitellus into its large subenteric enclosure, the abdominal walls, as we shall see ultimately, entirely encompassing the yolk. In some forms the yolk persists less prominently than in others, the somatopleure more rapidly extending ventrally and enveloping it. It never projects, as in Elasmobranchs and Sauropsida, in the form of a dilated sac distinctly separated from the ventral surface of the body, except at one point, where a narrow vitelline stalk still connects the two. Lereboullet speaks of such a pedicle in *Esox* (No. 95, p. 612); but this has not been confirmed, and in no case probably does the splanchnopleure surround the yolk, and form a narrow pedicel, until the latter has diminished to a very large extent.

Epiblast.—The external epiblast undergoes little change. We have seen that it is established as a single layer of cells, which very early become flattened and in section spindle-shaped. They form, in fact, an epidermis or corneous stratum, *ep*; but are not for some time marked off with any distinctness from the lower-layer cells of the blastoderm.* In the region of the head they first show their characteristic features; but they retain their primary rounded, polygonal outline at the posterior extremity of the embryo till much later (Pl. IV. fig. 5*c*). These last-named cells, as remarked on a prior page, are not differentiated fully from the cells beneath until the closure of the blastopore. While over the trunk, and the area of the blastoderm beyond, the corneous epiblast extends as a single stratum of squamous cells, yet it may often show slight proliferation, and present more than one layer. In section, through the head of an early flounder (Pl. IV. fig. 3), this is so, though it is true the protrusion of the optic vesicles may have cut off a thin superior stratum of neurodermal epiblast. Over the blastoderm generally a single layer of corneous epiblast seems to be present; the nervous layer, on the contrary, is many-layered, and in the middle line becomes so dense as to form

* In some Teleosteans this distinction would seem to be well marked, for Kowalewsky speaks of it as distinguishable soon after cleavage is ended in *Carassius*, *Polyacanthus*, and *Gobius* (*op. cit.*, 1886).

the thickened carina, *ne*, which presses upon the yolk (*vide* Pl. IV. fig 4). Very often it is so distinctly separated from the epidermal cells above, that a fissure intervenes, forming at the sides quite a spacious interstice (Pl. III. fig. 2). The cells of the neurochord are full and rounded (*ne*, Pl. IV. fig. 4), but as downward proliferation proceeds, those forming its lateral boundary become columnar, and unmistakably mark off the neurochord from the adjacent cells, especially in the fore part of the trunk. In this region the cells so rapidly proliferate ventrally and laterally, that they come into direct contact with the limiting hypoblast, *hy*, below and at the sides, or at most permit a mere trace of mesoblast to find a place there. Further back (Pl. IV. figs. 5*a* and 5*b*) the mesoblastic plates, *mes*, lie upon each side, and its ventral ridge alone touches the hypoblast, *hy*, while above it is limited only by the flattened stratum of epiblast, *ep*. Both layers of epiblast seem to extend over the blastoderm, and form the outer stratum of the yolk-sac, while below lies the extended hypoblast, which rests directly upon the periblastic cortex of the yolk. It is below the second epiblastic layer, which here assumes the character of a loose *mucosa*, a *rete Malpighii*—or rather in the lowest stratrum of this mucous layer, that the pigment occurs as amorphous bodies which extend over the surface of the yolk. In *P. platessa* and other forms, in which the epiblast lies immediately upon the periblast, the hypoblast being apparently absent, the pigment may send processes into the yolk-cortex; indeed pigment may develop in the periblast itself as described on a subsequent page.

Notochord.—In the earliest sections of the trunk, no trace of the notochord is seen, the neurochord, *ne*, being limited below by the single layer of hypoblast, *hy*, and having the thick mesoblast, *mes*, upon each side (Pl. IV. figs. 5*a*–5*d*). About the time that the lip of the blastopore has reached the equator, a median mass of cells (*nc*, Pl. III. fig. 11) intervenes between the keel of the neurochord, *nec*, and the hypoblastic stratum, *hyp*. These (notochordal) cells are rounded, and rapidly show a somewhat concentric arrangement, quite unlike the depressed cells of the stratified neurochord above (Pl. III. fig. 11; Pl. IV. fig. 5*b*). The notochordal cells, *nc*, it is true, are not separated by any definite line of demarcation from the ventral ridge of the neurochord, *ne*; but as the cells of the latter are unmistakably squeezed upwards by the pressure of the notochord below, this could hardly happen were the cells of the notochord a downward proliferation of neurochordal cells. The ventral ridge of the neurochord is evidently indented and its cells greatly flattened by these axial cells below. In such a section of the early notochord as shown in Pl. III. fig. 11, the possibility remains that this axial rod of cells is a remnant of median mesoblast, left when the lateral mesoblastic plates are sundered as protovertebræ, but the difficulty of such derivation lies in the fact that the mesoblast never appears to be confluent in this region; on the contrary, when once the notochord is indicated, it is sharply marked off from the mesoblast on either side. Thus in the section (Pl. IV. fig. 10), while the notochordal mass, *nc*, is not clearly separated from the hypoblast, *hy*, below, or from the epiblast (neurochord), *ne*, above, a very distinct line of division passes between it and the lateral mesoblastic plates, *mes*,

though in another section of the same date (Pl. III. fig. 13) the notochord and mesoblast are not distinctly separated.* In the chick the early notochord is continuous laterally both with the mesoblast and hypoblast (No. 19, p. 185); while VAN BAMBEKE, in agreement with OELLACHER, decides from his sections that the notochord is directly mesoblastic (No. 114; also see his fig. 14, pl. iv.). A comparison of a large number of sections shows that the mesoblast, *mes*, is very clearly separated as two lateral plates, *e.g.*, as in Pl. IV. fig. 5*a*; but the notochord, even when detached from the hypoblast, and apparently in intimate connection with the epiblast (neurochord), is never united to the myotomes. The hypoblast, *hy*, it is noteworthy, is hardly distinguishable in this region, as though it had been almost entirely used up in the formation of the notochord, for at the sides it is well-defined. BALFOUR noticed a similar thinning out of the hypoblast, and he states that only by high powers could the continuity of the stratum be made out (No. 14, p. 683). VAN BAMBEKE again denies that the hypoblast exists here at all, affirming that the notochord is at first in direct contact with the periblast below (No. 20*a*, fig. 15, pl. ii.), a layer of cells being afterwards pushed in from each side, and thus separating the notochord from the cortex of the yolk. The character of the cells, on close examination, shows the distinguishing features insisted on earlier, viz., the (dorso-ventrally) depressed condition of the neurochordal cells, *ne*, and their arched stratified disposition; whereas those of the notochord do not exhibit these features, and the contrast is still more emphatic at a later stage. In addition to their rotund condition, the notochordal cells are seen in longitudinal section to have a transverse arrangement, such as would be produced by an antero-posterior pressure (*nc*, Pl. IV. fig. 15), and this is interesting as indicating, what we have already suggested was possible (see p. 729), viz., that the notochord may be pushed forward to a certain extent from the primitive streak.

Unlike the condition in Elasmobranchs, the notochord of Teleosteans is at first clearly differentiated in the mid-trunk or mesenteric region (Pl. XXII. fig. 12, *nc*), and gradually extends forward, ending indefinitely above the middle of the cardiac rudiment, as in *Motella vulgaris*, on the first or second day (Pl. V. fig. 8). It curves downward, and sometimes seems to turn slightly to the left, as in *T. gurnardus*, on the ninth day. A section through the otocystic region (Pl. IV. fig. 4) shows a mere trace of median hypoblastic proliferation, while in the post-mesenteric region the activity of the hypoblastic cells has resulted in the formation, not of a distinct notochord, but of an arch of columnar enteric cells bridging over a cavity (Pl. IV. fig. 5*b*), suggesting a condition identical with that represented in BALFOUR'S figure of this region in *Petromyzon* (No. 11, fig. 39, p. 86), in an Elasmobranch (No. 15, fig. 1, *c*, pl. xxix.), and in *Lacerta* (No. 14, figs. 2, 3, pl. xix.); while SCOTT and OSBORN'S figure of *Triton* (No. 147, fig. 5, pl. xx.) no less closely resembles it. The last-named observers clearly saw that the notochord originated from the upper wall of the alimentary canal, as is indicated in their figure just mentioned. The outgrowth of the notochord from this enteric roof, figured in Pl. IV. fig. 5*b*, is not actually seen, but

* In *Lepidosteus*, BALFOUR and PARKER noticed a similar sharp separation from the mesoblastic plates, while the hypoblast had more intimate relation to the notochord, but they could not decide as to its real origin.

it is demonstrated that where the hypoblastic cells are not converted into the enteric arch they proliferate to form the notochord anteriorly; while the notochordal cells, *nc*, originating in this way merge posteriorly in the enteric roof (Pl. IV. fig. 5*c*), precisely as they unite in Elasmobranchs (No. 15, p. 683).

The notochord arises then as a ridge, or median proliferation, of the hypoblast in the posterior portion of the mid-trunk; extending from that region, anteriorly, chiefly by a progressive proliferation of hypoblast below, but doubtless to some extent, as already mentioned, by a forward pressure of the hind part of the rod which is first formed. KÖLLIKER's view, that the notochord is continuous with the primitive streak (No. 81), from which latter mass of cells the mesoblast arises and progresses forward, is consonant with such a forward growth of the notochord in Teleosteans as we have indicated. While the mesoblastic origin of the notochord is not generally accepted, there remains a possible mode of origin which sections do not directly discountenance. If it is neither formed from mesoblast nor hypoblast, it may yet be an axial differentiation of lower-layer cells, constituting *in situ* a median rod, when the mesoblast plates are cut off laterally, and the neurochord is defined above. Such a derivation has much in its favour, if we consider such sections as are given in Pl. III. figs. 2 and 11, and it is the conclusion adopted by BALFOUR and DEIGHTON. In the case of the chick they found a median plate of cells, not as yet divided into mesoblast or hypoblast, together with a short column of cells originating from the primitive streak (No. 19, p. 186), and these form the notochord. In Cyclostomes (*Petromyzon*) the notochord is formed by a vertical reduplication of axial hypoblast-cells, as CALBERLA (No. 39) showed, and as BALFOUR confirmed (*vide* No. 11, p. 87, figs. 39, 40); but whether this holds true for the Elasmobranchs, or whether axial-layer cells, as above stated for the chick, form it, BALFOUR found himself unable to decide. This uncertainty in regard to the origin of the notochord is further shown by the fact that RUDWANER was of opinion that it arose from the epiblast; while KINGSLEY and CONN considered it hypoblastic, as also did CALBERLA for *Petromyzon*, *Syngnathus*, and *Rana*. BRAUN, again, held that in the parrots the notochord was mesoblastic.

In Teleosteans KUPFFER affirms the origin of the notochord to be one of the unsolved problems of embryology, and he declines to come to a decision on the question (No. 87, p. 222). We have pointed out, however, that its hypoblastic origin is most in accordance with the sections. The large cells (*nc*, Pl. IV. fig. 5*b*) above the primitive enteron, there is little doubt, are the first traces of the notochord, which further forward is already partially defined. Fig. 11, Pl. III., again, is most satisfactorily interpreted as demonstrating the meeting of cells from above (the neurochordal proliferation) with the notochordal cells (hypoblastic proliferation) below. The cells of this longitudinal rod, *nc*, present much the same features as the adjacent cells, *mes* and *hyp*, though the neurochordal cells, *ne*, above always exhibit a more or less depressed appearance. At its anterior end the notochord grows rapidly forward, and, as SCOTT found in *Petromyzon*, it extends beyond the hypoblast of the alimentary canal into the cephalic region. There is, in fact, an anterior proliferation of notochordal cells (No. 146, p. 145). We see that in a series of

sections (Pl. IV. figs. 5*b*–5*d*) through the posterior region during the early stages of the notochord *nc*, it widens out and becomes lost in the primitive streak (*prs*), or rather merges in the upper wall of the gut, both disappearing in the caudal mass of indifferent cells (*prs*, Pl. III. figs. 3 and 12), just as in *Lepidosteus* the notochord is not separated from the lateral mesoblast, nor the latter from the neurochord, posteriorly. When ultimately it is defined, and extends from its hind emargination to its oral termination (*nc*, Pl. V. fig. 4), its cells do not long retain their primitive condition. They are not, as in *Triton*, primarily large cells which divide into small cells, and again break up to form larger cells once more (No. 147, p. 467), but are cells of small diameter—agreeing with such as for the most part compose the embryonic trunk, and become larger by an increase of their substance. Thus in a haddock of the fourth day (*nc*, Pl. III. fig. 13) with the rim at the equator, they can only with difficulty be distinguished from the mesoblast-cells, *mes*, on each side; yet when the blastopore is just closing (fifth day, Pl. IV. fig. 10), these cells, *nc*, are conspicuous for their large size and rounded contour, while their tendency to assume a radial arrangement is marked. The larger size of the cells in transverse section must, no doubt, in some measure be due to the forward pressure mentioned on a previous page, for only three or four cells reach across the diameter of the notochord. In their smaller, earlier condition six to eight cells extend across the same diameter.

While the notochord is well defined posteriorly (*nc*, Pl. IV. fig. 10), save at its extreme aboral end (and Balfour and Parker found a similar obliteration of the notochord posteriorly in *Lepidosteus*),* anteriorly it is even more distinctly marked (*nc*, Pl. IV. fig. 11), though as yet no chordal membrane surrounds it. When the blastopore is closing the notochord does not reach as far as the pectoral region, but on the first or second day afterwards it extends quite to the point where the cardiac swelling appears (Pl. V. fig. 8). About the time that the lenses of the developing eyes are visible the oral end of the notochord is sufficiently well marked to exhibit the characteristic flexure in front of the heart; but at its aboral end it spreads out slightly, and vaguely terminates in the tail which is now defined and prominent (*nc*, Pl. XXIII. fig. 9; Pl. V. figs. 8 and 10). Transverse striations soon cross the notochord, due to the continued forward pressure of its cells from behind, and cells here and there are seen breaking down, so that discoidal plates, or rather irregular vertical septa separating intracellular chambers, are formed. From its oral to its aboral end a continuous series of these chambers appears, resembling the "interrupted pith" of botanists (*nc*, Pl. IV. fig. 12). The process of vacuolation, of the breaking down, and aggregation of flattened cells in serial fashion, is preceded by the assumption of a radial arrangement in the cells about to suffer alteration, their nuclei showing a centripetal movement, so that they are mainly found along the central line of the notochord (*nc*, Pl. IV. fig. 10, just as Oellacher represents in No. 114, Taf. iv. fig. xvi$_2$, &c.). The process in *Clupea*, according to Kupffer, is not such as we have described for our forms, for the refractive discs, he states, are formed by the confluence of minute granular particles in the primary cells as

* *Phil. Trans.*, 1882, ii. p. 365.

they become flattened. A simple series of these transverse divisions, termed by him "secondary cells," is formed, and in a longitudinal section of the notochord he figures the various stages (No. 87, Taf. iv. fig. 44). The irregular transverse septa in section (*nc*, Pl. IV. fig. 12), are, however, evidently due to the adhesion of the walls of the primary notochordal cells, and the confluence of their protoplasm to form large interstices.* These septa become still more desiccated, and form a fine but complex meshwork, the outermost portions of which constitute a limiting membrane. No such investment as the latter as yet exists, though at a very early stage in Elasmobranchs Balfour made out a special sheath, in fact, very soon after its formation (No. 11, p. 684). In Teleosteans the neurochord above, and the hypoblast beneath, are in direct contact with the constituent cells of the notochord during the early metamorphosis just described. A stratum of flattened mesoblastic cells, it is true, at so early a stage as fig. 12, Pl. IV., may clothe the sides of the chorda, *nc*, while a thickened layer of similar cells may intrude between it and the hypoblastic enteron, *g*, destined, no doubt, to contribute to the later perichordal sheath. This external mesoblast is probably the special sheath described by Lereboullet at an early phase in *Esox* (No. 93, p. 527); but at this stage the mass of cells is external to and independent of the notochord, which must be regarded as a naked cord of cells undergoing rapid vacuolation.

When vacuolation has proceeded so far that the mere transverse fissures of fig. 12, Pl. IV., become converted into the spacious chambers more or less rounded, especially in the caudal region (Pl. XV. fig. 4, *nc*), and subsequently into the more irregular spaces (Pl. XI. fig. 11, and Pl. XV. fig. 7, *nc*), those collapsed cells which are not included in the septa will be pushed outwards, and form, as in fact they do, a continuous circumscribing sheath. The process is purely one of vacuolation, and the breaking down of the boundaries of smaller cells to form larger ones. No dot-like aggregations, such as Kupffer describes, seem to take part in the process, nor do scattered yolk-spherules (Balfour, No. 11, p. 684) or oily elements occur (Lereboullet, No. 93, p. 527) in the contents of the notochordal cells. The contents of the cells are fluid, clear, and homogeneous, and often exhibit a slightly pinkish tint in certain lights, as in *T. gurnardus* on the fifth day. Lereboullet did not notice in his forms the early condition—the primary cells of the notochord, for it was already transversely striated when he first observed its structure; and he notes the remarkable feature, just referred to, that through all its substance oily elements are dispersed (No. 93, p. 527, pl. ii. fig. 44). With its increase in length the notochord grows in diameter, a condition which is precisely the opposite of that described by Scott and Osborn in *Triton*, for in that form the notochord is largest in cross-section during its earliest stages, and greatly diminishes in diameter during subsequent stages (No. 147, p. 467). The increase in diameter of the Teleostean notochord stretches the cells of the sheath, *i.e.*, the superficial cells of the chorda; thus they become

* These interstices, with fine membranous limits, form a series of discs placed one behind the other along the whole length of the chorda. They form large discoidal cells, which at many points do not entirely pass across the notochord, as they vary considerably in diameter.

very thin, and at times almost imperceptible (*nc*, Pl. VII. fig. 6). The true notochordal sheath during the later larval periods is very delicate and fine (Pl. VII. figs. 6, 6*a*), nor does it, as Balfour indicates (No. 11, p. 546), ever become thicker or more definite. It is nucleated (*n*, Pl. XV. fig. 7), as Gegenbaur showed in the greatly thickened sheath of *Salmo salar*;* but the nuclei are irregularly arranged, and in some sections they are so sparse as to suggest the presence of an enucleate stratum (*cs*, Pl. XV. fig. 7), though this condition is easily explained by its mode of origin. In horizontal sections of the chorda the flattened cells of the sheath overlap and produce a more or less regular tessellated appearance (Pl. XV. fig. 7). Kupffer says that this sheath in the herring is homogeneous and without nuclei (No. 87, p. 222), while he describes a round nucleus in each chamber of the vacuolated notochord. Such nuclei in our forms are rare, though sections often pass through the points, where several septa unite and produce the same appearance as nuclei in the septa would do, but they are simply sections of the junction of cell-walls, or, at times, merely the collapsed contents of the notochordal chambers.

Of the subnotochordal rod, which has been described by Balfour, Oellacher, Ryder, and others, nothing definite can be here stated. It would, in fact, not appear to be developed in the forms specially considered in this paper, though Ryder mentions it in *Alosa* and *Salmo* as a well-marked strand of cells; and Oellacher is of opinion that it shares in the development of the aorta along the under surface of the chorda dorsalis. The intruding mesoblast limiting the chorda below in the Gadoids, gurnard, and others is an indefinite lamella figured in its earliest condition in Pl. IV. figs. 12 and 18, which subsequently forms a median meshwork in which the early hæmal lacunæ are developed, while laterally the renal connective and other tissues are formed out of it (*vide* Pl. VII. figs. 1, 4, 6).†

Vertebral Column.—The vertebral column and its costal appendages belong as such to a stage subsequent to the larval condition proper, and, in this place, little more can be done than simply to touch upon certain points observed before the close of the first month after extrusion.

The cod and haddock will be mainly referred to, as the condition of the vertebral column shows great differences in various Teleosteans; in some forms cartilage-cells appearing, and cartilaginous arches developing soon after hatching, whereas in others no such elements are present until the embryo is about a month old. Lereboullet, indeed, was unable to make out any ossification in the perichordal sheath, in *Perca*, until the young fish was three months old (No. 93, p. 644).

The condition of the notochord before and after hatching has been described, and sections of *G. morrhua* or *G. æglefinus*, on the seventeenth to the twentieth day, show the same simple structure almost unchanged—the cuticular layer or nucleated chordal

* *Comp. Anat.*, Lond. 1878, fig. 221*b*, p. 427.

† The myotomes are broken up into fibres about the ninth day (two days before hatching in *P. flesus*). Eight or ten of these fibres, in horizontal section, are seen passing across the shorter axis of the myotome, which is rectangular, and measures about ·001 in. × ·0018 in., the longer measurement including the columnar external stratum of cells lying beneath the epiblast.

sheath proper (*cs*, Pl. XI. figs. 14, 15) being very thin, and the mesoblastic perichordal sheath (*pcs*) but little increased in thickness. This latter sheath, of protovertebral origin, is equivalent to the skeletogenous layer of Plagiostomes, though in them it is greatly thickened. In this perichordal sheath an outer lamina can be made out, especially when the rudiments of the vertebral bodies and arches are developed, as it forms their outer investment. Below the sheath and its elastica externa, a layer of cells in the sharks intrudes, coming, as Balfour thought, from the outside, and forming the cartilaginous tube around the chordal sheath. From this intruding layer the future vertebræ are formed, and it may be termed the inner skeletogenous layer: it is the inner half of the skeletogenous tube. Outside the membrana elastica externa, however, another mesoblastic layer is formed, viz., the outer half or outer skeletogenous layer from which the neural and hæmal arches are developed. In the less primitive sharks, such as *Mustelus*, the Rays, and others, the inner skeletogenous layer is much reduced, and the elastica externa is considerably nearer the chorda than in *Cestracion* and *Notidanus*. If we consider the process of reduction to have affected the external portion until no outer half exists, we can then look upon the perichordal sheath in Teleosteans as the inner half of the skeletogenous layer, reduced, but still bounded by its outer limiting layer, viz., the membrana elastica externa (*mel*, Pl. XI. figs. 14, 15). There is, of course, difficulty in separating the parts of a sheath so thin as that surrounding the notochord in Teleosteans, but in a few forms, *e.g.*, *Cyclopterus*, in which cartilage develops somewhat precociously in the vertebral column, large chondral cells appear in this external layer, which passes upward, and over the spinal cord as a membrana reuniens superior. The cells likewise ascend up each side of the cord, forming the rami of the neural arch. Similarly the ventral arch is developed. In many forms, however, the arches and outer osseous laminæ of the vertebral bodies are not preceded by preformed cartilage. In such cases (*e.g.*, *Gastrosteus*) the osseous matter is clear, homogeneous, and brittle (Pouchet's "spicular substance," Kölliker's "osteoid matter"), and exactly resembles in its chitinous appearance the clavicular portion of the pectoral girdle, and the maxillary elements of the upper jaw. The presence or absence of this spicular substance seemed to Kölliker of diagnostic value for classificatory purposes, but as Pouchet points out (No. 119, p. 274), both spicular substance and osteoplastic tissue may occur in the same form. Pouchet states, and seems to be the first to do so, that in some cases osteoid processes, and in other cases cartilage, with osteoplasts, form the superior and inferior vertebral arches. But whether arising as bars of regularly disposed chondroplasts, or as homogeneous spicular deposits, the vertebral bodies, and their projecting dorsal and ventral rami, are the products of the perichordal sheath, and arise within its definite limiting layer. The view that the main part of the sheath in Teleosteans is a thickened membrana elastica interna, and derived from the cells of the chorda itself, is not supported by sections, inasmuch as the hypoblastic notochordal sheath always remains extremely thin, and even when well developed, as in the Salmonoids, is still merely a single stratum of flattened cells. In Elasmobranchs W. Müller recognised an elastica interna closely investing the

chordal sheath, and BALFOUR refers to both layers as closely adherent, though distinct, but the former apparently decreases in thickness, and is then difficult to see (No. 15, vol. xi. p. 421). From the mesoblastic perichordal sheath alone the vertebral bodies originate, while its outer limiting stratum (the elastica externa) gives origin to the arches. The neural arches precede the hæmal in development; no trace, in fact, of the ventral processes being discernible when the neural arches project some distance dorsally.

Of course, in a degenerate skeletogenous layer, such as the Teleostean perichordal sheath, the identification of the precise layers, seen more favourably in other fishes, is attended with much difficulty; and one of us, in attempting to distinguish the different laminæ, has referred to the outer layer as a "limitans externa" (No. 122, p. 454); indeed, the opinion expressed that the existence of an "elastica externa" in Teleosts, is a doubtful point, is supported by the fact that such a membrane does not properly exist in Amphibians, as well as in the *Amniota*. Favourable sections of Teleostean embryos, especially such a form as *Cyclopterus*, bear out, however, the above interpretation, the external layer being very distinct. Outside the perichordal sheath itself in post-embryonic stages plates of spicular substance develop. Thus in a young but mature specimen of *Pleuronectes*, the oral end of the notochord is seen to have acquired such a spicular sheath—formed apparently in the connective tissue outside the external limiting membrane—a distinct interspace separating the plate from the perichordal sheath. Four rami of the same chitinous substance project, one pair dorsally and one pair ventrally, and are well seen in sections through the otocystic region.

Branchial System.—The head of the Teleostean embryo consists, as already indicated, of an expanded mass, chiefly neurochordal, or rather brain-tissue, and separated from the cortex of the yolk below by a thin layer of hypoblast (*hy*, Pl. III. fig. 1). The hypoblast forms here the roof of the sub-oral cavity, which has no floor, or rather, its floor is simply the periblast enveloping the yolk. Behind and below the ears a large oval area is apparently pushed in, resulting in the perforation of the lateral epiblast on each side of the otocystic region, these fenestræ (*poa*) communicating with the primitive mouth-chamber within (Pl. VIII. figs. 3, 4). This opening, which may be called a primitive opercular opening (*poa*), though the true operculum is a new and later growth, is plainly visible in *Molva vulgaris* on the fourth day, along with a number of superficial irregularities, doubtless connected with the active changes going on at this point in connection with the branchial arches (Pl. X. fig. 6). The significance and function of this cleft (Spritzloch) upon each side is not readily understood, as the œsophageal lumen is not apparently open in front, and any perivitelline fluid which gains access to the sub-cephalic chamber, probably cannot find passage into the alimentary canal. HOFFMAN, however, speaks of it as produced by an evagination of the œsophagus, at first below the otocyst, but shifting forward and opening in front of the ear (No. 69, p. 7; *vide* his pl. i. fig. 5, *emb. sp.*, also fig. 3, on p. 7). These embryonic "Spritzlocher," he says, are merely transient structures, and the interesting question is raised as to whether they may be a reminiscence of the outer or extra-branchial system of the Cyclostomes, of which traces

are observable in the Elasmobranchs. Each aperture, *poa*, has a strongly marked corrugated border or fold, which sweeps in a graceful curve round the opening, and passes forward beneath the otocysts (*au*, Pl. VIII. fig. 4), for in pelagic forms, the shifting of which HOFFMAN speaks was not observed, and in front the fold is gradually lost. The opercular flap is a much later outgrowth from the tympanic region, apparently a fold of the integument, which protrudes, and grows backward over the gill-slits (*opc*, Pl. XI. figs. 10, 11). Below the hind-brain and otocysts, the hypoblast shows great increase in its cells, so that by the time the heart is defined it forms a thick supra-cardial plate (Pl. XI. figs. 2, 7, 8), beneath which mesoblastic cells make their way by a downward growth of the lateral cephalic masses. The sub-cephalic floor of hypoblast and mesoblast is limited below by a somewhat ill-defined layer of nucleated periblast (*per*, Pl. XI. fig. 8). The mesoblast thus intruding into the oral hypoblast becomes columnar, and forms paired rod-like masses (Pl. XI. figs. 5, 6, 7). The cells are concentrically arranged along the axis of the transverse bars. LEREBOULLET evidently refers to the downward growth of mesoblast, and speaks of it as a ventral lamella (*i.e.*, splanchnopleure), out of which, he adds, is formed later "the maxillary and hyoidean elements, and the gill-supports." While the appearance of serial mesoblastic thickenings along the floor of the pharynx is a marked feature in Teleosteans some days before emerging from the egg, their disposition and conformation are very difficult to make out. There is indeed considerable variation in the condition of the branchial region, and this is especially seen in newly-hatched gurnards. Usually three branchial bars are visible (Pl. VIII. fig. 8) as pale structureless bands, with intervening cellular tissue, and passing transversely towards the mesial ventral line beneath the otocysts. BALFOUR and PARKER (No. 18) noticed in *Lepidosteus*, six days after fertilisation, two transverse streaks on either side of the hind-brain. From a comparison with the sturgeon they judged them to be branchial clefts, but in section these clefts could not be detected. In the early condition of the branchial system the study of sections is by no means easy. C. VOGT shows, in an embryo of *Coregonus palæa*, thirty-six days old, branchial vessels, but indicates no skeletal bars (*vide* No. 155, Taf. ii. fig. 58). The fact seems to be that, soon after the arches are distinctly formed as definite bars, a vessel, or rather a long thread-like lacuna, is formed along the posterior margin of each bar (Pl. XI. figs. 9, 11). Five transverse bands, sometimes an indication of a sixth, extend later on each side across the floor of the wide and flattened œsophagus, from a point just behind the eye to a little distance beyond the otocyst, so that the floor becomes raised into a series of cross-ridges which cease in the middle line, and between the ridges the hypoblast is pushed so that the mesoblastic ridges gradually become separated by hypoblastic septa. PARKER speaks of these ridges as separated by the dehiscence of the thinned interspaces between them (No. 117), but this hardly describes the process correctly, the rib-like thickenings being more truly separated by the paired hypoblastic diverticula or septa, these being pushed out from the sides and floor of the pharynx and affecting the differentiation of the serial gill-arches. Dehiscence takes place, it is true, but much later, and it results in the formation of

actual slits, a phenomenon not seen until long after the arches are fully differentiated. From this protrusion of enteric hypoblast, SEDGWICK likened these paired pouches to nephridia; indeed, he considers them homologous, the kidney-system of vertebrates never overlapping them, but commencing behind their posterior limits (No. 148, p. 67). The clefts or gill-openings are probably not formed until some time after extrusion from the egg, but the hypoblastic diverticula indicate their future position, and the dense mesoblastic masses between them form the branchial skeleton or gill-arches. The latter in their early condition appear as a series of rounded or subquadrate structures, when seen from below (Pl. VIII. fig. 5), but viewed from the side fine striations merely are observed passing dorso-ventrally with a slight inclination forward, these striations being the linear outpushings of the oral hypoblast (Pl. VIII. fig. 6). The arches thus early indicated are not simultaneous, and LEREBOULLET observed in the embryo of *Perca* that they appeared successively from behind forward (No. 93, p. 616). The precise stage when the branchial clefts are open cannot be stated. There is no doubt it is very late, for long after the arches are clearly defined the slits are still unformed, even in so advanced an embryo as *Gastrosteus* (Pl. XI. fig. 9), in which the mouth is open, while the hypoblastic cells, *hy*, which pass down between and surround the bars, *bra*, still form a continuous layer. A fifth branchial arch can be made out, but remains rudimentary in the Gadoids and other forms here considered; while anterior to the four branchial arches proper, two pairs of stout bars are developed at an early stage, viz., the hyoid (*hy*, Pl. X. figs. 2, 3; Pl. XIII. figs. 5, 6), and in front the mandibular (*mn*,—MECKEL's cartilage). Both these arches undergo a more complex development than the branchial rods behind, and with the appearance of cartilage-cells, both are readily distinguished by their greater length and stoutness, as well as by their direction, both extending forward and tending rapidly to complete the arch on the floor of the mouth. The upper portion of the first or mandibular arch becomes expanded (Pl. IX. fig. 6; Pl. XIII. fig. 5); and PARKER speaks of it as well marked in the salmon (No. 117, p. 113), splitting longitudinally into two, giving origin in this way to a fore part, the mandible proper, and a hind portion, the hyoid. In our forms the hyoid is already well developed when the division of the mandibular cartilage takes place, and it would appear therefore that the posterior portion, *hm*, which is the stronger, and much expanded at its upper extremity, is really the hyomandibular, thus arising as an element separate from the hyoid, while the narrower anterior part, *pq*, also split off, becomes the palato-quadrate. Before this splitting is complete, the extended lower part separates as the primary lower jaw or mandible, *mn*, and its proximal part becomes enlarged (Pl. IX. figs. 6, 7; Pl. X. figs. 2, 3), to afford an articulating surface for the two suspensory elements above, the palato-quadrate and the hyomandibular, which separately articulate, the former doing so earlier than the latter, and more directly (Pl. IX. fig. 7). From the proximal portion of the mandible an anterior process grows out at a subsequent stage (Pl. IX. fig. 7), while in the angle below the end of the stout and broad hyomandibular, a small element, the angular, develops. The forward growth of the palato-quadrate cartilage must be a late phenomenon, for the pre-

maxillæ and maxillæ develop in advanced embryos as paired translucent rods (Pl. XI. fig. 20), which gracefully curve, like bars of chitin, below the eyes forward to the ethmoidal region, and form the sole lateral supports of the oral roof (Pl. X. fig. 1; Pl. XIII. fig. 7). They are essentially superficial, and lie in a thin stratum of membrane which stains deeply, called by Pouchet "tissue générateur," and occupying the situation of Parker's "subocular bands," though he regards them as the rudiments of the pterygo-palatine arch (No. 117, p. 113). The homology of these dermal maxillary rods, with the labial cartilages of more primitive forms, as suggested by Dr Günther (No. 61, p. 90), is of much interest. A pair of curved bars, probably palatine elements, are also developed in the roof of the oral chamber at a late embryonic stage. They are irregular in thickness, slightly curved, and attenuated at the extremities (Pl. XI. fig. 18).

When first distinguishable, the pharyngeal bars consist simply of solid mesoblastic thickenings passing along the lateral and ventral walls of the mouth, and more or less oblique in direction; moreover, in cross-section, these thickenings are found to be paired, and united in the middle line, forming a roof over the pericardial chamber (Pl. XI. figs. 1–3, 6–8). The cells assume a columnar arrangement, and constitute laminæ, which appear as parallel superposed strata, when the bar is cut longitudinally (Pl. XI. fig. 9), but in a cross-section of a bar these strata are observed to be somewhat concentric and laminated (Pl. XI. figs. 6–8). Each rudiment of a branchial arch (*fg*, Pl. XI. figs. 6–8), when fairly defined, consists of a cylindrical mass of cells, concentrically arranged round the central point of the bar, and limited above by the epithelial hypoblast of the pharynx, and below by the pericardial hypoblast. They increase in length, and change from the transverse to the antero-posterior oblique position (Pl. VIII. fig. 9), the inner extremity of each pair of arches apparently shifting forward, so that they point anteriorly (Pl. X. figs. 2, 3, 5); while their upper and posterior parts, which extend up the lateral walls of the pharynx, have moved very slightly from their primary position. Neither the mandibular nor the hyoidean arches are so markedly transverse in situation as the branchial bars proper, and they alter very little in position as development proceeds. In the gurnard, three days old, at the anterior end of the hyoid arches, *i.e.*, where the copula is formed, a large boss occurs, formed chiefly by a free development of the lining membrane of the oral floor. This membranous expansion (really a lingual rudiment) projects as a large irregular elevation on the floor of the mouth, and is lifted up by the erratic movements of the hyoid arch, as though the operation of deglutition were being performed (Pl. XIV. fig. 2). Gradually the arches lose their dense indifferent appearance, and become converted into cartilage, the small primary cells being broken down, so that each bar consists of larger flattened elements placed transversely, and giving the arches a transversely striated appearance (Pl. IX. fig. 5). The flattened cells become hyaline, and each arch shows a single column of hyaline discs contained in a thin perichondrial membrane. The first two arches wholly assume this character, and are seen to be composed of these discs or chondroplasts placed one above the other along the whole length of each bar (see the figure just referred to); but in the four arches which

follow, only a portion undergoes this change, viz., that part of each bar nearest the pharyngeal cavity, *i.e.*, throughout the entire upper part of each. The rest of the bar remains indifferent in structure until a tubular cavity is formed from end to end. This tube at first is apparently single, but later is divided by a delicate septum into two tubes, an upper arterial and a lower venous trunk. External to and below the hæmal canals the loose epithelial covering of the bar becomes nodulate, a double row of papillæ projecting on the posterior and ventral side of each arch. The appearance of these gill-rudiments is thus preceded by a considerable interval by the conversion of the arches into cartilage, as LEREBOULLET observed in *Perca* (No. 93, p. 623), the same author noting in that species the growth of the gill-tubercles from the soft cellular membrane covering the gill-arches (see his plate iii. fig. 7). Moreover, he speaks of them as hollow (p. 627), an appearance probably due to the intrusion of mesoblast into each papilla, which is thus provided with a mesoblastic core and a hypoblastic epithelial covering.

The formation of these branchial tubercles belongs, it may almost be said, to the first post-larval stages, and their subsequent development into the branchial fringes of the adult leads beyond the present limits.*

The further development of the early cartilages may be easily followed in a large chondral element such as the hyomandibular, or the massive mandible itself. The disc-like chondroplasts which form a single column along the entire length of the bar (Pl. IX. fig. 5), slightly alter in form, becoming wedge-shaped when seen laterally, and lie over each other in an alternate manner, as though about to separate into two rows,—sometimes, indeed, a disc becomes thin in its median part, and divides, resulting in two wedge-shaped chondroplasts. Thus the original single column of chondroplasts becomes broader, and exhibits two or more rows (Pl. IX. fig. 7). In the mandible this change affects the upper or articular portion, while the anterior growing part, which continues to lengthen until the cartilages of each side meet at the tip of the extended oral floor, still maintains its simple columnar character, and consists of a single series of chondroplasts. In other cases, as POUCHET noted (No. 119, p. 296), the chondroplasts towards the extremities lose their disc-like form—becoming irregular in outline and mingling with the enveloping tissue—just as in the limbs of young Amphibians. In the region of the joints, as in the upper or articular portion of the mandible, the chondroplasts become irregular, numerous, and disposed round the joint conformably to the contour of the articulating element (Pl. IX. fig. 7). The development of a crest is due to the protrusion of similar small irregular chondroplasts, which grow out, row upon row, as a strong lamella. POUCHET regards these new chondroplasts as not due so much to fission of existing chondroplasts as to development from the nuclei, so plentiful in the perichondrium or "tissu générateur" which clothes the bars (No. 119, p. 298). These nuclei he describes as crowded at the margin, and, as they pass inward, become separated by the intrusion of the hyaline matrix.

* In *Esox* and *Perca* the yolk has decreased and its circulation has been almost obliterated, according to LEREBOULLET, when the gills are formed (No. 93, pp. 613, 627).

In the young cod, three weeks after hatching, the branchial system is wholly converted into cartilage, and forms a complex series of translucent hyaline bars, in which the four parts—the epi-, cerato-, hypo-, and basi-branchial pieces can be distinguished, and the small rod-like azygos pieces in the middle of the oral floor form the several copulæ for the respective arches.

In *T. gurnardus*, and other pelagic forms, the cartilages of the jaws apparently become stiff and immobile about the eighth day after hatching, and the hyoidean apparatus also shows no regular movements. The fish, however, by its forward jerking motion, drives water into the widely-open mouth, and aeration is thus easily effected, for the opercular opening is broad, and the operculum itself projects outward and backward, as a thick flap of the integument.

The mandibular rami, *mn*, continue to lengthen upon each side to such a degree that they project much beyond the upper jaw, and a symphysis is formed at the anterior margin (Pl. X. figs. 1–5). No feature is more striking than this extraordinary development of the lower jaw, and in sickly and abnormal embryos it produces the most fantastic appearances—the protruding mandibles frequently curving downward, so that the gape of the young fish is remarkably wide (Pl. XIV. fig. 2), and even in normal examples this extension of the floor of the mouth, and the mobility of the lingual and hyoidean structures, increase the oral aperture very much (Pl. X. figs. 1–3, 5, 5*a*), and contribute doubtless to facilitate the capture of the minute organisms which form the earliest food of the young Teleostean.

Skull.—The capsule enclosing the brain is, like the rest of the body of the embryo, simply a thin epiblastic layer composed of the flattened corneous stratum, and the thicker sensory remnant beneath.

Between this ectodermal covering, *ep*, which though expanded in the form of a bulbous protective capsule, can scarcely be regarded as a cranium, and the brain-mass below, a space intervenes occupied by a transparent substance, apparently of a jelly-like consistency. This space, *ss*, filled with fluid, is inconsiderable during the earliest stages within the ovum (Pl. XIX. fig. 10), and even in a newly-hatched fish (*ss*, Pl. VIII. fig. 6), above the mid-brain, *mb* (optic vesicles), it is small, though larger in front (between the nasal capsules), *fb*, and behind, *hb* (over the cerebellum and fourth ventricle); but it increases at the end of the first week (Pl. VIII. fig. 7), and during the second or third week after extrusion it becomes enormously enlarged, and imparts to the more advanced embryos a very grotesque appearance (*ss*, Pl. XII. figs. 2, 6; Pl. XVI. figs. 1, 3, 5). Often this sub-epidermal enlargement abnormally develops, and embryos with the cephalic region remarkably swollen are not uncommon—fig. 3, Pl. XVI. being probably such an example; but under ordinary conditions the enlargement is considerable, and median sensory papillæ appear in it, immediately beneath the corneous layer, with connecting nervous filaments passing downward, probably to the lateral sensory tract (*sno*, Pl. XVII. fig. 1).

At an early stage the mesoblast of the head consists of a thin stratum chiefly aggregated between the eyes and the neurochord (*mes*, Pl. IV. fig. 17), while, above, the brain

is directly in contact with the inner surface of the epiblast. Later, however, this mesoblastic tissue extends and finds its way into the lateral sinuosities of the brain-surface, and it passes upward as a thin membrane composed of much flattened cells, which finally more or less completely invests the brain. The relation of the two is very intimate, and probably the pia mater is at this time separated, though any differentiation into distinct strata cannot be made out in the membranous investment (*mes*, Pl. IV. figs. 14, 21). From this layer, however, the three membranes—dura mater, arachnoid, and pia mater—are ultimately differentiated. On its inner surface pigment rapidly develops, as early, indeed, as the fourth day after fertilisation in some forms (*p*, Pl. IV. fig. 13). We have thus a double covering over the brain, for to the simple ectodermal layer (*ep*, fig. 14), which primarily covers the neurula, there is added a thickened mesoblastic membrane (*mes*), constituting the primitive membranous cranium (Pl. IV. fig. 21; Pl. XXIII. figs. 1, 2, 3*a*; Pl. XXIV. figs. 3, 5, 6). Meanwhile changes are proceeding at the base of the brain, and whereas it at first lay almost directly upon the yolk (Pl. IV. figs. 3, 4), separated only by a thin layer of hypoblast (*hy*), it now rests upon a floor of mesoblast (Pl. IV. fig. 21). This mesoblast is apparently an extension forward of the pectoral mesoblast, which pushes anteriorly as the notochord advances, and when the latter finally terminates beneath the mid-brain, a plate of intruding mesoblast is seen extending upon each side of it and passing as a thin sheet beneath the fore-brain.

At the fore end of the notochord quite a dense plate is formed (Pl. XI. fig. 2), and a thickened continuation of this mesoblast passes beneath the eyes, forming a projecting ridge of epiblast with a core of mesoblast (Pl. XI. figs. 2, 3), which is doubtless PARKER'S "sub-ocular band" (No. 117, p. 119). These two ridges form on each side a lateral flap or curtain, and the head is thus raised slightly from proximity to the yolk. As already pointed out, before an actual oral slit appears, an oral cavity exists whose roof slopes considerably on each side, and meeting in the middle line forms a highly arched chamber. A section through this acutely angular cavity in the region of the posterior prosencephalon (thalamencephalon) shows the apex, so to speak, marked by a small and solid mass of cells, a cylindrical rod in fact, which in sections further forward is found to flatten out in the form of a bilobed plate, strongly suggesting the union and depression of two cylinders of cells. We see then at this early stage, about the time of hatching, that the base of the brain is strengthened by two parachordal masses, which lie on each side of the notochord at its oral end, *e.g.*, in the section of *Anarrhichas* (Pl. XXIV. fig. 3), and form a dense basilar plate, while further forward the flattened parachordals cease, and in their place two thin cylinders, the trabeculæ, can be distinguished (Pl. XXIV. figs. 5, 6), which, as just pointed out, unite and form beneath the thalamencephalon a single rod.* This rod again expands beneath and in front of the

* The early appearance of the trabeculæ is noteworthy when connected with the early development of the neural arches in the trunk. PARKER'S view that the trabeculæ are ventral arches of the vertebral column, serially followed behind by the branchial arches, has been much disputed, and the early appearance of the neural arches of the vertebral column is opposed to PARKER'S view.

fore-brain, to terminate in a pair of large flattened lateral horns, and an internasal plate centrally (Pl. XI. fig. 11). These early skeletal structures are the first indications of the cartilaginous cranium, but as yet they are formed of closely-aggregated cells, which stain deeply, and on account of their density are readily distinguished from the adjacent mesoblastic cells out of which they have been differentiated. Whether their cells break down or not is difficult to make out, but they undoubtedly become antero-posteriorly flattened, and in cross-section the rods under consideration begin to assume a more translucent appearance, due to the discoidal character of the constituent cells. Within a week or ten days after hatching, these elements are converted into clear boldly-marked nucleated cartilage-cells. The large parachordals as they become cartilaginous extend outward, and meet to coalesce with the dense cartilaginous floor of the auditory capsules (Pl. VI. fig. 9; Pl. XXIII. fig. 2). The trabeculæ between the eyes contract, and approach the base of the brain in the region near the infundibulum—becoming very narrow as the roof of the brain expands. Further forward the trabeculæ, however, spread out, forming a large anterior plate of cartilage, slightly thinner medially, and more thickened laterally, *i.e.*, in the portion forming the cornu (Pl. XI. fig. 11).

While cartilage thus abundantly develops in the skull, no trace of it is seen in the axial skeleton of the trunk—metameric aggregations of mesoblastic cells (Pouchet's "tissu générateur") alone indicating the points along the notochord where the future vertebræ will be formed. During this time also cartilage appears in the form of four small plates around each eye, all with a concave surface towards that organ, and formed of large cartilage-cells placed over the summit of the eye—beneath and on the anterior and posterior surfaces. Whether the first or supraorbital cartilage expands later to form the tegmen cranii, and the second to form suborbital elements, while of the remaining two one becomes the lachrymal, and the other or postorbital becomes alisphenoid and post-frontal, though probable, could not be determined from an embryo in the second or third week after hatching. About the middle of the third week, indeed, four series of cartilages may be distinguished—(1) the posterior basal, (2) the posterior lateral (auditory), (3) the anterior lateral (optic), and (4) the anterior basal.

The first named constitutes the basis cranii proper (parachordal and occipital elements); the second includes a basal auditory plate (Pl. VI. figs. 9, 10), very dense and massive, and affording an outer articular surface for the hyomandibular (*hm*), and probably consisting of opisthotic and pro-otic elements, as yet undifferentiated. Above the ear a small aggregation of cartilage-cells (*epot*, Pl. VI. fig. 3) occurs, from which the epiotic and supra-occipital are probably formed, while the third series are in a condition too early to identify, and are best regarded simply as circumorbital cartilages developed at four separate centres on the surface of the sclerotic membrane. The fourth and last series occurring at this stage are the trabeculæ, with their expanded internasal element and the curved lateral cornua. Into the theoretical question of the significance of these paired basal bars it is here unnecessary to enter.

Of the further changes in the skull and facial elements little can be said, as at the end

of the first month the young embryo shows little further modification. The development of translucent spicular plates upon the surface of the more exposed bones, especially of the face, is a noteworthy feature in the young fish, but belongs to the post-larval period. It may be noted, however, that these homogeneous spicular plates are not solely of dermal origin—in fact, they develop as a thin outer layer of the true cartilaginous elements, and arise within the nucleated perichondrium.

The connective-tissue septa of certain muscles which are much used, become changed into thin rods of clear spicular substance, a median rod, for example, passing up beneath the pericardial cavity, and forming a fulcrum for the retractor hyoidei muscles. A similar bar occurs also between the genio-hyoidei.

Brain.—The anterior enlarged portion of the neurochord, of which frequent mention has already been made, is really the brain. It extends the whole depth of the fore-region of the embryo, forming a somewhat rhomboidal mass, rounded above, deeply carinate below, and arched over by the epiblastic integument, while it is limited ventrally by the hypoblast (Pl. IV. figs. 3, 4). The growth of the large optic vesicles, as two massive ellipsoidal bodies (*op*, Pl. IV. figs. 14, 16), protruding laterally from this region, is an early and notable feature; but the details will be considered later, with the sensory organs. The part which becomes the mid-brain (*mb*, Pl. IV. figs. 16, 17) is very early distinguished by its greater breadth and volume from the narrower and prominent snout (*fb*), while the hind or metencephalic part (*hb*) gradually passes away into the neurochord (*ne*) of the trunk. No division as yet separates the encephalic from the spinal portion of the neurochord, and the former is distinguished only by its increased breadth and depth. It is remarkable, too, as extending fully one-third the total length of the embryo in its early condition. No transverse cerebral folds appear until about four-fifths of the yolk are enveloped, when a cleft, very obliquely directed, appears on each side of the post-optic region. An anterior portion—the united mid- and fore-brain—can now be distinguished from the hind-brain (*hb*). The latter is, very shortly after, separated by a similar though less marked fold from the nervous cord (*ne*) behind. Lereboullet noticed this early transverse folding, which he says is due to the brain becoming doubled upon itself; but he erroneously supposed that the cleft first formed is the metencephalic, instead of the mesencephalic, and further conceived the neural tract to consist of two parallel tubes. These becoming folded, produce two vertical projections, which he calls the cerebellar lamellæ (No. 93, p. 533). It is really the cerebral fold, the cerebellum being, as just stated, marked off slightly later. The mid-brain, lastly, is constricted off by an interorbital fold, so to speak, and the three regions of the brain are now defined (Pl. IV. fig. 17). Reference has already been made to the dorsal or medullary groove; but it is at this stage, when the brain is separable into cerebellum and united mid- and fore-brain, that this groove often appears in a very marked manner. Thus, in *T. gurnardus*, on the fourth day, a deep median fissure may be seen—the sides of which slope at an angle of about 70°. It is a temporary groove, as previously pointed out, and not apparently connected with the subsequent cerebro-spinal canal. Soon after the closure of the blastopore,

sometimes a little earlier, a fine cleft (*mc*) appears by separation of the median cells of the encephalon along a vertical longitudinal plane. It commences in the mid-brain, and passes into the fore-brain, extending almost to the anterior limits of the latter (Pl. IV. fig. 17). This is the first indication of the true neural canal. It passes dorsally, ceasing before reaching the upper surface of the brain, and ventrally, leaving below a thick tract of nervous cells uncleft. The early brain thus becomes incompletely divided, as RYDER aptly expresses it, into "two flat thick plates of cells placed vertically between the eyes" (No. 141, p. 503). At its anterior termination the canal sends off two lateral vertical continuations, forming a cruciform fissure which marks off the fore-brain (*fb*, Pl. IV. fig. 17; Pl. VI. fig. 6); while in the mid-brain, as the fissure ascends, it bifurcates laterally and horizontally, so that the lumen of the mesencephalon, in cross section, is T-shaped (Pl. IV. fig. 21), the roof being thinner than the walls and floor, which are very dense, a feature better seen in sections of *Anarrhichas* (Pl. XXIV. figs. 3, 6). No continuity of the central canal with the lumina of the optic vesicles seems to be completely established, and certainly no trace of such a connection is observed in sections at this stage. The canal now rapidly extends posteriorly into the trunk, and as it does so vertical lateral cavities are sent off, one pair in front of the cerebral fold, forming the optic ventricle or *Iter a tertio ad quartum ventriculum*, and a second pair, constituting the fourth ventricle, immediately posterior to the cerebellar fold (*cb*, Pl. VI. fig. 6). The most notable feature at this early stage is the continued lateral extension of the mesencephalon (*mb*), and its progress backward over the metencephalon (*cb*), until it almost covers the latter with its two broad lobes, which continue to increase in breadth (compare figs. 5 and 7, Pl. VI.). Between the eyes we have, therefore, a prominent mesencephalic dome formed of two halves, narrower in front, but broad and overlapping the narrower posterior fore-brain (thalamencephalon) and the base of the mid-brain. Several days before hatching this extension of the mid-brain takes place, the T-shaped chamber (optic ventricle) increasing in its upper portion and its lateral regions until the roof above exhibits a considerable decrease in thickness and a marked columnar disposition of its cells.

An embryo before hatching usually shows such a development of the mid-brain as above described (*vide* Pl. XIV. figs. 1, 2), and the brain-mass as a whole exhibits that separation and arrangement of its parts which permanently remain in Teleosteans. The mesencephalon embraces the largest extent of the brain, and by its prominence above imparts that rounded bulbous form to the head which is so characteristic of the young fish (Pl. VI. fig. 7; Pl. VIII. figs. 6, 7, 10; Pl. XIII. figs. 1, 5, 6; Pl. XIV. figs. 2, 4). Thus the medulla oblongata (*mo*), with the anterior transverse fold or cerebellum, forms a hind-brain plate of triangular shape, the mid-brain (*mb*) constitutes a similar triangular mass, and both have their broader sides or bases towards each other (Pl. VI. fig. 6), just as KUPFFER describes in *Clupea* (No. 87, p. 220). The cerebellum is almost entirely covered by the posterior enlargements of the optic lobes (*op*, Pl. VI. fig. 7), but it protrudes distinctly as a thickened ridge passing across the front end of

the fourth ventricle. A very thin roof continues from the cerebellum and covers the medulla oblongata, whose triangular floor is becoming better defined and dorso-ventrally deeper. Laterally the cerebellum (*cb*) does not break continuity with the double fold of the mesencephalon (*mb*), of which, indeed, it appears to be merely a thickened posterior portion or third fold (Pl. VI. figs. 5, 6). This fact has led many anatomists to deny to this fold the name of cerebellum. MM. Philipeaux and Vulpian regard it as merely a third lobe of the optic mass, and they, with many others who follow Weber (*Anatomia comparata nervi sympathici*, Leipzig, 1817), regard the two swellings passing along each side of the medulla oblongata, and composed of grey vesicular matter, as the cerebellum. MM. Philipeaux and Vulpian emphasise the view that the cerebellum consists of the two hollow lateral masses which flank that part of the optic mass usually called cerebellum (No. 118, p. 171). More recently Miklucho-Maclay has urged a similar view regarding the Elasmobranch brain, and he interprets the prominent anterior portions of the corpora restiformia as the true cerebellum. Beneath the cerebellum the medulla continues forward and merges in the basal region of the thalamencephalon, and even in this early condition distinctly turns upward, the curvature becoming marked somewhat later (Pl. XXIV. figs. 1, 2). Ryder states that in *Alosa* this upward bend is not indicated (No. 141, p. 504), but it is probably a notable feature in most Teleosteans. Dohrn, for instance, indicates it in *Belone* and the Lophobranchs, and the result of it is that the fore-brain is brought down below the front termination of the medulla oblongata, and a false cranial flexure is thus effected. The actual relations, in regard to position, of the brain-vesicles to, say the notochord, are not altered, nor does the head-region externally present a marked flexure downward (Pl. XIII. figs. 1, 5); yet a longitudinal section through the brain shows, as in the section of *Anarrhichas* (Pl. XXIV. fig. 2), the mesencephalon raised up, while the prosencephalic region bends down. If we follow the course of the medullary canal, we find in front of the cerebellum a marked ascent—the hollow optic lobes occupying a much higher plane than the thalamencephalon and the hemispheres, and the result is that, without the remarkable shifting forward of the parts of the brain seen in the chick, the prosencephalon comes to lie on the ventral side of the medulla and cerebellum. This modified flexure, which is not comparable to the true and extensive bending down of the prosencephalon, *e.g.*, of Elasmobranchs, has this simple explanation, that without any very obvious displacement of the other parts of the brain, the floor of the myelencephalon and metencephalon are flexed upward, and, as a consequence, the mesencephalon is raised, and the thalamencephalon and hemispheres come to occupy a distinctly ventral position. This false flexure persists even after the embryo has emerged from the ovum, but with the fuller development of the oral region it is at a later post-larval stage corrected.

The remarkable displacement just described does not change the external aspect of the embryo. The mid-brain still occupies the summit of the head—its greater prominence being due to the process of median upheaval from below, which brings the lateral margins of the optic lobes into proximity inferiorly with the eyes. The optic

lobes, as before stated, laterally overlap the basal region of the mid-brain, at an early stage; but this superposition is now considerably increased—indeed, it reaches fully to the middle lateral line behind the eyes (Pl. XXIV. fig. 3). The fore-brain still forms a narrow, laterally compressed mass projecting anteriorly to form the round snout or face of the embryo. Its bulk is less than half that of the mid-brain, and it encloses a small dorsal chamber (Pl. XXIV. fig. 5). The prosencephalic floor is very dense, the side walls less so, while the roof thins out greatly. A small fissure continued from the chamber above passes into and partially divides the thick floor of the fore-brain; but sections of this region show a condition much in contrast with the capacious hollow vesicle of the Elasmobranch fore-brain. Several folds appear on the superficial aspect of the fore-brain (Pl. VIII. fig. 6) about the time of hatching or even before: but not until the second or third day after emerging does the deep fold appear which divides the fore-brain into two parts, the cerebral or anterior fore-brain and the thalamencephalic or posterior fore-brain (Pl. VI. fig. 7). A longitudinal fold passes over the dorsal surface of the fore-brain (*fb*) before it is markedly separated into front and hind prosencephalic regions, and it thus becomes longitudinally bifid at an early stage (Pl. VI. fig. 6). No olfactory lobes proper exist as yet; indeed, as MARSHALL found in Salmonoid larvæ, these structures must be comparatively late in appearing.

The changes which ensue when the primitive brain of three vesicles is finally divided into a series of five, are very complex and difficult to follow; but the main features may be indicated. The five parts of the brain distinguished are as follows:—

Prosencephalon,	(1) Anterior fore-brain or cerebral hemispheres, &c. ("Vorderhirn," GEGENBAUR and BAER). (2) Posterior fore-brain or thalami optici ("Zwischenhirn," BAER).
Mesencephalon,	(3) Mid-brain, or optic lobes, &c. (Mittelhirn, BAER, Zwischenhirn, GEGENBAUR).
Metencephalon,	(4) Hind-brain or cerebellum (Hinterhirn, BAER, Mittelhirn, GEGENBAUR).
Myelencephalon,	(5) Medulla oblongata (Nachhirn, GEGENBAUR).

From the fourth ventricle a narrow fissure, the aqueductus Sylvii, leads into the third. The base of the latter partly overlies, and partly abuts against, the mass now separated, as already indicated, from the cerebral hemispheres or anterior fore-brain by a transverse superficial cleft (Pl. XIII. fig. 1). This posterior portion of the fore-brain is the thalamencephalon, and it is the part of the brain which, for the most part, overlies the roof of the mouth.

Very early a portion of the hind part of the thalamencephalic floor is directed backward as a prolongation beneath the elevated medulla oblongata, and during its course its direction is slightly downward. The cells composing this encephalic diverticulum have a somewhat columnar arrangement, and surround a cavity continuous above with the third

ventricle. The structure thus formed is the hollow infundibulum (*inf*, Pl. XXIV. fig. 1), which abuts on the roof of the oral cavity below, though the two remain separate. The anterior part of this basal region gives origin to the optic nerves, which will be considered under the sense-organs. A chamber, or rather a loose meshwork of cells (Pl. XXIV. fig. 1), most probably hypoblastic, though possibly mesoblastic, lies behind the infundibulum, and into this loose mass the oral end of the notochord (*no*) pushes as it bends downward. In some sections the notochord and infundibulum are brought into closer contact. The elevation of the oral roof too is very distinctly marked at this time, and such probably (see Pl. XXIV. figs. 5, 6) corresponds to the curvature produced in Elasmobranchs by the acute cranial flexure characteristic of those fishes and higher forms. On the summit of this arch a mass of cells appears, evidently a proliferation of the oral roof-cells rather than a diverticulum. This ovoid mass is the pituitary body (*pt*, Pl. XXIV. fig. 1). It lies in front of the infundibulum, and from its origin is in close relation to the base of the thalamencephalon. The precise origin of this body in these forms is difficult to make out, but its cells, as Hoffman has clearly shown in the salmon and trout, are indistinguishable from the oral epithelium.* A small median swelling, not unlike the hypophysis in structure, lies in front of the latter—that is, behind and slightly under the point where the optic nerves decussate. When further advanced such appears to form the hypoaria or lobi inferiores—so well developed in Percoids, and their special ventricles in the adult communicate with the lumen of the infundibulum. The anterior fore-brain and the mid-brain at a very early stage so far overlap the intervening mass (the thalamencephalon) that only a small portion of its roof is superficially exposed (Pl. XXIV. fig. 1). This small extent of roof becomes very thin, as does also the roof of the anterior fore-brain, and it is much folded. In a transverse section through the mid-portion of the thalamencephalon before its walls have thinned out, a central aggregation of cells can be distinctly observed, and this soon exhibits a marked concentric arrangement, and become slowly pushed out as a papilliform process (Pl. VIII. fig. 6). A lumen develops at a later time, and it communicates with the (third) ventricle below. Its cells, which were rounded and not dissimilar to the adjacent cells of the thalamencephalic roof at this time, assume a columnar disposition, and it now forms that very prominent and interesting structure in young fishes—the pineal gland. The primary rounded or conical form is not long retained; it either becomes truncated, *i.e.*, depressed, or more or less plicated, and pressed against the thin developing arachnoid membrane, which alone separates it from the integument. In the salmon and trout Hoffman gives a slightly different account of its origin. It arises, he says, as a true evagination, not a solid protuberance, and its lumen is continuous with a portion of the ventricle below distinctly marked off as a special recessus infra-pinealis (No. 69, pp. 100, 102). Moreover, its cells are at first epithelial in character and columnar,

* Dohrn states that the hypophysis makes its first appearance at the same time as the endodermal evaginations of the oral and branchial clefts. It arises as a pair of more or less distinct pouches much anterior to the paired oral slits.

whereas the rounded form is only assumed later when the cells have increased in number, and form two or three layers (No. 69, p. 103; *cf.* figs. 9, 12, Taf. iv.). Much later, when the absorption of the yolk is accomplished, the lumen of the epiphysis becomes obliterated, and it is separated off as an oval, lobed, or deeply folded solid mass of cells (No. 69, p. 103, Taf. iv. fig. 17).

The spinal cord, when fairly advanced, proceeds quite to the termination of the notochord, but its general features call for no detailed description. Usually the terminal filum is very delicate and attenuated; but at times a remarkable enlargement is observed. This final nervous swelling was very well seen in a young embryo of *Motella mustela* (Pl. XV. fig. 4, *ne*), but in other forms it was also made out, *e.g.*, *Cottus scorpius* (Pl. XIII. fig. 2) and *Molva vulgaris* (Pl. V. fig. 7).

Auditory Organs.—The otocysts are very early differentiated—that is, about the same time that the lens of the eye is invaginated and defined (as pointed out by Kupffer, No. 88), *i.e.*, in many pelagic forms about the fourth to the sixth day after fertilisation. In *Salmo salar*, according to Parker, the ears are pushed in from the outside shortly before hatching; and he refers to these "auditory involutions" as "still widely open" during his "first stage" (No. 117, p. 113). This description, however, is quite unlike the mode of formation in the Teleosteans specially referred to in this paper; and Lereboullet's account, in the case of *Esox lucius*, is certainly more in accordance with observations at St Andrews, where he says that the early ears "are two small spheres, symmetrically placed, and formed by the grouping of plastic elements, ... at first solid; but becoming hollow, and transforming into the auditory capsules" (No. 93, p. 529). The otocysts are, in fact, not involutions of the external epiblast, but solid proliferations of the sensory or neurodermal epiblast (*au*, Pl. IV. figs. 4, 11, 16*a*). In *Lepidosteus* Balfour and Parker describe the ear as originating from the under or sensory layer, but as a hollow thickening, over which the epidermic layer is externally continuous (No. 18); and Hoffman, while he rightly speaks of this external layer as extending unbroken over the otocyst, says that the otocyst itself is formed as a hollow invagination of the under-layer (Grundschicht), a condition not exhibited by our sections of pelagic embryos. The earliest phase seems to be that of a rounded mass just becoming visible in the early haddock, *i.e.*, a solid proliferation of the sensory stratum (*conf.* Pl. IV. fig. 11, the figure referred to, with Hoffman's, No. 69, figs. 3 and 4, Taf. i., and fig. 1, Taf. iv.), in which very soon a radial arrangement of cells can be made out preparatory to the formation of a lumen. The latter rapidly appears (*au*, Pl. IV. fig. 13; Pl. V. fig. 8), and is at first minute and spherical, but soon enlarges to form a spacious ellipsoidal chamber (*au*, Pl. VI. figs. 5, 6), very obtusely rounded, depressed laterally, and with its inner wall abutting against the neurochord (*ne*), while on its outer side, and superiorly, it is separated from the exterior only by the tegumentary epiblast (*ep*). The walls of the otocyst are very dense when the lumen is small (*au*, Pl. IV. fig. 13), but they apparently stretch as the chamber expands, and become comparatively thin (*au*, Pl. V. fig. 9; Pl. VI. figs. 1, 2, 7). Lereboullet

noticed that, as the auditory vesicles elongate, "a mass of yellowish granules" appeared in them prior to the formation of the true otoliths (No. 93, p. 529). The contents of the otocysts seem, however, to be clear, homogeneous, and without granules in our forms, but usually before the end of the first week, and within twenty-four hours after the lumen in each is defined, two minute calcareous bodies appear on the floor, usually towards each extremity of the longer axis of the otocyst (*oto*, Pl. VI. fig. 5; Pl. XII. figs. 1–5). These otoliths have the appearance of two very small dense grains, and are, as Dr CARPENTER remarks (No. 37), similar in character and mode of formation to the concretionary spheroids common in the urine of the horse, the integument of the shrimp, and other forms. It is well known that when a solution of lime-salt in gum-arabic is slowly decomposed, carbonate of lime is deposited in spheroidal concretions. Sometimes, as Mr RAINEY found, two of these will unite in dumb-bell form, and occasionally a number will unite in the form of a mulberry (No. 126, p. 19).* The walls of each otocyst are composed of columnar or rather spindle-shaped cells, and at first over much of their surface several layers are superposed (Pl. VI. figs. 3, 4). Subsequent changes, however, not only affect the thickness of the walls, and cause them to thin out, but alter their contour. Moreover, being pressed in, from above, anteriorly, the otocyst (*au*) when viewed from the side, loses its angular elliptical shape, and has more or less the outline of an oyster-shell (Pl. VIII. figs. 4, 6, 8, 9; also Pl. XII. figs. 1–4, 7). A ridge also appears on the floor, caused apparently by some of the internal nervous tissue being aggregated along the shorter axis of the capsule (Pl. VIII. fig. 8). In *Esox*, about the time the cardiac chamber is formed, and the embryo rises erect upon the yolk, the otocysts, according to LEREBOULLET, become more transparent, and have a thick investment like cartilage (No. 93, p. 529). No such investment appears in our forms until very much later, the walls retaining their original cellular structure (Pl. VI. figs. 3, 4), though at certain points they become thickened, sensory cushions (*neu*) being formed of large fusiform cells, which take a slightly radial disposition. An embryo of *T. gurnardus*, six days after hatching, shows three such nervous aggregations provided with erect motionless cilia or palpocils. That situated upon the floor is by far the largest, but it may vary somewhat in outline as well as position. The remaining two are anterior and posterior (Pl. VI. fig. 2). In one specimen, viz., the example figured, a dorsal hernia (*x*) or process of the cellular wall occurred. A long trumpet-shaped tunnel (*can*) passed anteriorly and superiorly, the inner end being faintly granular and botryoidal in appearance from the irregularity of its cells. In some forms the ears become so enormously developed that they may nearly meet in the middle dorsal line, or may, as PARKER describes in *Salmo*, actually overlap the posterior border of the eyes (No. 117, p. 113). In the gunnel (*au*, Pl. XIII. figs. 5–7) they are certainly very much larger at a comparatively early stage than in any other form reared at St Andrews, and they may

* A still more striking example of definite concretions in a clear fluid is that afforded by certain Annelids, *e.g.*, the stylets of the Nemerteans. LEREBOULLET proved their calcareous nature in fishes; he says—"Treated with acid, they effervesce and disappear. No membrane is left, or it is too thin to distinguish" (No. 93, p. 633).

be larger and more rapidly developed in the embryos of demersal ova than in pelagic forms, though in the clupeoids with both demersal and pelagic ova the spacious nature of the otocysts is a characteristic feature.

It is difficult to follow the changes in the structure of the ear in the transparent living fish, on account of its complexity. The semicircular canals seem to be developed primarily from thickenings of the cellular lining of the auditory sac, like the nervous cushions, a soft hernia being produced which grows inward as an increasing ridge, in which a cavity is formed, as shown in Pl. VI. fig. 10, *can.* Viewed from the side, at a later stage the semicircular canals protrude into the chamber of the otocyst as three short knobbed processes directed inward from the margin. The median and inferior canals end abruptly in the middle of the chamber. Frequently the otoliths, instead of lying apart, each in a depression of the auditory floor, may shift, so as to lie towards the same part of the otocyst, *e.g.*, in the anterior depression, as in Pl. VI. fig. 7, and Pl. XII. fig. 7. At times three otoliths occur, and when two are present, as is normally the case, there is usually a marked disparity in size, Lereboullet remarking that in *Perca fluviatilis* the posterior otolith acquires a diameter triple that of the anterior (No. 93, p. 632).

In preparations very deeply stained with hæmatoxylin the otoliths not only show the usual glistening crystalline structure with radial striations (*oto*, Pl. VI. figs. 2, 3, 4, 9), but less numerous concentric striations, and a very marked dark central core surrounded by an external stratum, which stains more faintly (Pl. VI. fig. 11).

A further stage in the development of the Teleostean ear is observed in the young flounder (Pl. XV. fig. 8), in which the disparity of the otoliths and the complex condition of the auditory chamber are well shown.

Olfactory Nerves and Pits.—The olfactory pits are distinguishable on the sixth day or later, *i.e.*, about the time that the heart's pulsations commence. They are produced by a paired thickening of the sensory epiblast (ep^2, Pl. IV. fig. 17) in front of the upper part of the hemispheres. Each soon forms a flattened oval sac of slightly elongated cells (*ol*, Pl. IV. fig. 2), beyond which a small portion of the fore-brain (*fb*) extends (Pl. IV. fig. 1). A depression commences from the outside, and each nasal sac becomes a cup-like structure, whose cells are now fusiform and radially arranged (*ol*, Pl. IV. fig. 17). The flattened corneous layer is no longer present at the two points where the pits are formed, and as they become deeper and the walls of each sac increase in thickness, they may be brought into close contact with the anterior fore-brain, upon whose front they seem to lie in the living embryo (Pl. VI. figs. 6, 7, 8, 10; see also Pl. XII. figs. 1, 3, 7, and Pl. XIII. figs. 1, 3, 5, 6, 7). So small is the space at this time separating the sacs from the brain that it is difficult to detect the nerve-strand which connects them. Hoffman, however, made out the origin of the olfactory nerves as minute proliferations of the wall of the anterior fore-brain (No. 69, p. 87). This minute outgrowth, on reaching the nasal sac, coalesces with the proximal surface of the nasal pit. No olfactory lobes are at this time discernible; indeed, Marshall doubts whether in the Teleosteans

(Salmonoids) he examined true olfactory lobes ever are formed. At any rate, he cannot regard them, and justifiably so, as embryonic structures (No. 100, p. 313). The proximity of the olfactory pits and the brain renders the determination of such a point in the minute Teleostean forms here considered very difficult; but MARSHALL'S conclusions admit of little question. In the Elasmobranch-embryo the olfactory lobes are not distinguished until almost all the features of the adult are attained (BALFOUR'S stage O) (No. 100, *vide* pl. xiv. figs. 24, 33, 34), and in the chick they cannot be made out until the seventh day (No. 17, p. 162). There is no trace of these lobes in *Rana* during the earlier stages, according to MARSHALL, and the nerve-strand passing to the olfactory pit is very short.

A similar condition is found in Teleosteans; a solid strand of cells passes from the roof of the fore-brain, before it shows any trace of external division, to the pits (*ol*, Pl. IV. fig. 16), and these latter as they increase in bulk approach, as in Pl. IV. fig. 17, and come into such close proximity to the fore-brain (*fb*) that an actual reduction in length of the primitive nerve results, so that it is barely distinguishable (Pl. VI. fig. 6). The histological character of these primary olfactory strands supports the view that they are merely diverticula from the brain, in which organ no fibres are yet formed, for the first pair of nerves have a similar solid cellular structure. This structure MARSHALL found to be retained, when the other cranial nerves had assumed the fibrillar character. It is remarkable that the olfactory nerves, which are amongst the earliest to be given off, retain their primitive structure longest. MARSHALL could not make out any ganglionic enlargement (No. 100, p. 312); but BEARD in some later researches found that, as in *Rana*, a ganglion does arise in connection with the epiblastic thickening forming the pit, and that the olfactory nerve itself is also split off from the skin (*vide* his figs. of *Rana* and *Rhodeus amarus*, figs. 3 and 4, pl. viii. No. 22). The dorsal position of the nasal pits is interesting, as in the Elasmobranchii and Aves these structures are on the under side of the head. The nerves shift down from their first position, and are found to connect with the fore-brain ventrally (1, Pl. XXIV. fig. 4; also *vide* MARSHALL, No. 100, pl. xiv. fig. 33). Of course in the Teleosteans this transference is much reduced, as the fore-brain does not grow so extensively as the hinder portions of the brain; but MARSHALL has undoubtedly given accurately the facts of the early development of the first pair of nerves, which, however, HUXLEY considered to be developed late, and to have but one paired connection with the brain, and that a ventral connection (No. 74, p. 71). This ventral origin is secondary, and comparatively late, but it is very much later before the basal swellings known as the olfactory lobes are clearly indicated (Pl. XXIV. fig. 4).

In the early forms treated of in this section the division of the original single nasal opening into two was not followed. It is readily observed in the wolf-fish (*Anarrhichas*)* and in the young flounder (Pl. XV. fig. 8).

Optic Nerves and Vesicles.—One of the earliest features in the development of the

* *Vide* section xiii. p. 254.

Teleostean embryo, as already noted, is the enormous development of the anterior cephalic region, which is chiefly due to the protrusion of two rounded lateral masses from the sides of the narrow fore-brain (Pl. V. fig. 1, *op*), and not, as LEREBOULLET stated, from the walls of the mid-brain (No. 93, p. 522). The pair of massive bulbs thus formed are rapidly defined as the ellipsoidal optic vesicles, the first of the sensory organs to appear. In section (Pl. IV. fig. 16) the cells of the neurochord, at a point midway between the dorsal and the ventral surface, actively push their way outward, and pass for the most part upward, so that a pair of stalked vesicles are formed, lying against the sides of the fore-brain—not quite upright, but placed at an angle which brings the lower and smaller lobe in proximity, while the upper and much larger lobe is pushed away from the brain (Pl. IV. fig. 3). Sections clearly demonstrate the abundant protrusion of cells to form the optic bulbs, which KINGSLEY and CONN regard as formed in the main by a constriction or fissure commencing above and behind the lateral enlargement, and progressing forward and downward (No. 78, p. 207), but the constriction which they carefully describe is preceded by a very apparent bulbous outgrowth. These protruded cells are indistinguishable in size or contour from the neurochordal cells which gave them origin, but the outer limiting layer of cells assumes a columnar disposition, as also does a double plate of cells along the median dorso-ventral plane. This latter feature has been referred to (No. 122, p. 452) as a radial disposition of the central cells and "as though about to dehisce along a central vertical plane in order to form a median chamber, longitudinally placed;" but a chamber converting the solid optic proliferations into capacious hollow vesicles, such as the early condition of these structures is generally described, is never completed—a very narrow fissure being all that is usually formed, and even this may at times fail to be developed before the invagination of epiblast presses the outer layer against the inner layer of the primitive optic vesicle. RYDER describes and figures the narrow fissure referred to (No. 141, p. 499, pl. v. figs. 26, 27); and in section (Pl. IV. fig. 17) it is plainly seen as a slit in the midst of the optic vesicle. This separation of the median cells is interesting, for, though the Teleostean eye is not pushed out as a chambered sac from a hollow brain-vesicle, as is the primitive mode of origin, it secondarily acquires a trace of this vesicular condition. In the living embryo it rarely presents more than the character of a delicate median line or slit in the optic bulb (Pl. V. fig. 1). Pl. IV. fig. 3, shows the first indication of this slit-like lumen, which can be traced along the short thick stalk into the fore-brain, where it is lost. In horizontal section we see that while the cells—pushed out to form the optic vesicle—in the main pass upward, they also extend posteriorly, carrying the vesicle some distance behind its pedicel or point of origin: the optic vesicles on their appearance are thus defined most distinctly behind. Each vesicle, in fact, forms a depressed pyriform body, which by its smaller end remains attached to the brain, while the swollen upper portion extends dorsally, backward and distally (Pl. IV. fig. 16). SCHENK, who first gave a full account in his well-known researches on the eye of fishes (No. 143), seems not to have recognised the fact that the eye and the entire central nervous system in

these forms is primarily solid and without a lumen. KUPFFER appears to have been the first to describe the true condition (No. 88).

It is important to notice that the nerves—that is, the stalks of the optic vesicles—arise at a different level from the olfactory and other nerves, a fact inconsistent with the derivation of the nerves from a ridge or "sinnesplate," such as GÖTTE and others distinguish. A dorsal stratum of neurochordal cells may perhaps be regarded as a neural crest from which the posterior nerves spring, but such a crest does not pass further forward than the hind-brain; the first and second pair of cranial nerves, as will be seen, arise, the one primarily as dorsal and the other as lateral median evaginations of the prosencephalon. In pushing backward the optic vesicles shut off a thin stratum probably of mesoblast which later forms an enveloping cup, and gives origin to some important structures in the developing eye. This mesoblast (*mes*, Pl. IV. fig. 17) is probably a forward growth from the thin plate of the same layer in the otocystic region (Pl. IV. figs. 16, 17). Meanwhile, the short, thick connecting stalk becomes constricted, and the vesicle itself alters both in form and position. Viewed from the side, the latter is now almost perfectly elliptical (*op.*, Pl. XXII. fig. 12), and is nearly perpendicular in position, *i.e.*, parallel to the vertical axial plane of the embryo (Pl. V. figs. 3, 10). The columnar cells along the central vertical plane of each vesicle (Pl. IV. fig. 3) separate sufficiently to mark a slight but distinct fissure (Pl. IV. fig. 17; Pl. V. fig. 1). This fissure persists when the optic vesicles have altered their position, so that they lean by their upper portion against the neurochord, and this median chamber, instead of passing upward, outward, and posteriorly, as when first indicated (Pl. V. fig. 1), now passes downward and outward (*op*, Pl. IV. fig. 14). As already indicated, the pyriform outline is almost wholly lost, the optic vesicles lying obliquely against the fore and mid-brain—as elliptical bodies laterally flattened, and traversed by a vertical lumen longitudinally separating each into an inner and an outer half, the latter layer being very much thicker than the inner half (Pl. IV. fig. 17). This condition does not remain long. Before the end of the day these "primitive optic vesicles" become indented by the pressure of the epiblast lying external to them, the deeper layer of which becomes rapidly thickened so as to form in section (Pl. IV. fig. 17) an almond-shaped mass on each side, pressing upon the central region of each optic vesicle (*op*), which gradually becomes cup-shaped, the hollow of the cup being occupied by the thickened mass of epiblast, which forms a dense spherical body, the lens (*l*, Pl. IV. fig. 14). The optic cup or secondary optic vesicle becomes thinner marginally, and this portion creeps round to the outer side of the lens (Pl. IV. fig. 21), forming a circular lip around it, which is incomplete on the lower side. This gap, the choroidal fissure, is very distinctly seen at this stage (*ch*, Pl. VIII. figs. 6, 7, 8; Pl. IX. figs. 1, 3; Pl. XII. figs. 1, 2), and it persists for some time (Pl. XVI. fig. 1).

The mesoblastic cells, which were included as a thin plate between the optic vesicle and the brain (*mes*, Pl. IV. fig. 17), have spread over the former as an outer layer (Pl. IV. fig. 21), and pushed their way through the choroidal fissure into the interior chamber of the eye, as is seen in section (Pl. IV. fig. 20). A similar horizontal

section, at a lower plane (Pl. IV. fig. 19), shows the fissure disappearing. These intruding mesoblastic cells (*mes*) appear to become packed between the lens and the retinal surface of the optic cup, and doubtless break down to constitute the vitreous humour of the adult eye, forming also, as some observers think, the "*capsula hyaloidea*," in which a rich vascular network afterwards develops. The differentiation of the cellular optic vesicle into its various layers has already taken place before the embryo has emerged from the ovum. The formation of these layers can, however, only be very briefly touched upon.*

We have seen that the eye, soon after its appearance as a solid bulbous protrusion (*op*, Pl. IV. fig. 16), separates by a slight fissure into two layers, constituting the primary vesicle (Pl. IV. fig. 17). With the obliteration of the lumen, the two layers become closely apposed, and the eye consists of a thick-walled cup of undifferentiated cells (Pl. IV. figs. 14, 21), whose chamber—the lumen of the secondary vesicle—is closed in front by the growing lens (*l*). An investing layer of mesoblast (*mes*) forms the sclerotico-choroidal sheath, absent, however, from the front of the eye. As the time for extrusion approaches, scattered pigment-spots occur outside the optic vesicle and in the external investment. These spots are unbranched amorphous particles, sparsely distributed as an irregular pigment-layer over the whole surface of the optic cup, save in front of the aperture of the pupil (Pl. XIV. fig. 1; Pl. XVII. fig. 10). On each side of the lens they are densely aggregated (Pl. V. fig. 6; Pl. XVI. fig. 8). The outermost layer of the cellular vesicle, *i.e.*, the stratum of cells internal to the layer of pigment, assumes a marked columnar character (Pl. XI. figs. 6–8)—bold striæ passing across it, and dividing it into wedge-shaped radiate masses as indicated in Pl. XXIII. fig. 3*a*. At the same time the cells within, constituting the main bulk of the vesicle, separate, though somewhat obscurely, into two layers of great and almost equal thickness—the inner layer being slightly thicker (in section) than the outer. The line of separation is delicate and indistinct at first, but subsequently develops into a fine molecular band—the prominent internal molecular layer. The inner surface of the columnar stratum shows a delicate membrane, possibly the posterior or membrana limitans externa ("limitans interna" of Hoffman, No. 69, p. 50).† From the outer stratum consisting of columnar elements the rods and cones are developed, while the two thick inner layers with their intervening lamina give rise to the other layers of the retina. Such is the condition of the six layers of the retina shortly before the time of hatching in pelagic forms, *e.g.*, the cod and the haddock. In other forms, chiefly demersal, which reach a somewhat advanced embryonic stage while within the ovum, the eye attains a much further degree of development.

A haddock, on the second or third day after extrusion, shows additional changes, the second layer being better marked, as is also the inner molecular layer, though both are still very thin laminæ. The columnar character of the bacillar stratum is still more

* The minute description of the development of the Teleostean eye is in the able hands of Dr Marcus Gunn, one of the surgeons at Moorfields.

† This layer Dr Gunn has identified as the "external molecular layer"—a "thin dark finely granular line;" and should this be so, then the "*limitans externa*" must be developed at a much later stage, as Dr Gunn states.—*Vide Ann. Nat. Hist.*, Sept. 1888, p. 268.

distinct. During the first week after hatching, the internal molecular layer undergoes great development, and rapidly becomes a thick and bold stratum separating the external granular layer from the internal granular layer. The external molecular stratum is slowly differentiated on the inner surface of the columnar layer, while the inner granular layer shows, though very obscurely, a separation into an inner and an outer portion. The pigment of the choroid is much more abundant than before, and in the living embryo gives to the eyes a dense appearance, so that the minute transparent fish can usually be discerned in the tanks of the laboratory by the two large dark eyes, which form a most prominent feature (Pl. XVI. figs. 3, 6, 7,* 9 ; Pl. XVIII. figs. 1, 2). The structure of the retina exhibits little further change during the later larval stages, but in the post-larval conditions other features appear, which need not be noticed in detail by us, as Dr Marcus Gunn has specially occupied himself with this subject. Thus in a young flounder, still transparent and colourless, the pigment-layer is greatly increased in thickness, and it sends prolongations into the bacillary layer. The cylindrical rods form a very distinct stratum, while the flask-shaped cones are well defined, and present a contrast to the corresponding layer in Amphibians, which have a very insignificant stratum of cones. Indeed, as Max Schultze pointed out, this layer in Teleosteans recalls the condition in the Mammalian retina (No. 144, *vide* sect. iv. of his paper). The double disposition (twin-cones) in the adult eye of osseous fishes has not yet been assumed, so far as can be made out. The striking coloured globules so prominently seen in this layer in Batrachians, birds, and some reptiles are absent, nor do they at any subsequent stage appear to be developed. That Teleosteans should have a layer of rods and cones so early and so well developed, whereas in Selachians (and cartilaginous fishes generally, it is said) no cones can be made out, is a remarkable circumstance. Bats, hedgehogs, and other nocturnal forms amongst Mammals, are destitute of cones.

The limitans externa in the post-larval stages is a very delicate lamina ; but it is well defined. The external granular stratum now consists of several layers of large cells separated from the inner granular layer by a comparatively broad external molecular layer.

The inner granular layer itself Hoffman separates into three portions—an outer thin stratum of "tangentiale Fulcrumzellen," a "medialer Theil der inneren Körnerschicht," and a "lateraler Theil" of the same layer. In the flounder, as well as in such forms as *Cottus* and *Cyclopterus*, only the outer "tangential" cells can be distinguished from the remaining elements of the inner granular layer, which form a very thick band. Internal to the last-named layer is the internal molecular stratum, anterior to which the ganglionic layer can be distinguished. The internal molecular layer Hulke describes as including a large quantity of connective tissue, in the midst of the fibres of which are large branched corpuscles of very considerable dimensions (No. 71, p. 247), but in comparatively late post-larval stages no trace of these structures can be made out. The

* Mr Cunningham's figure (*op. cit.*, pl. vi. fig. 4) appears to be, as he supposes, this species, viz., *Liparis Montagui*.

ganglionic layer is composed of large cells, which form a remarkably broad layer—quite unlike the narrow ganglionic stratum in the Salmonidæ. Anteriorly it is defined by the fibres of the optic nerve, and the limitans interna (HOFFMAN'S "limitans externa") or anterior limiting membrane, which forms the lining of the optic globe. Some observers look upon this membrane as the hyaloid capsule of the vitreous humour; HULKE, however, regards it as a separate membrane, and such it would appear to be, since it precedes the formation of the vitreous fluid by a long interval (*vide* No. 71, p. 248). An anterior annulus, the lip of the secondary optic vesicle or cup, remains unaffected by these histological changes, and a mass of indifferent cells fills up the interspace between the retina proper and the circular curtain—the extension of the choroid in front of the eye. These cells are in fact involved in the formation of the iris and ciliary ridges, the ciliary muscles being developed from the mesoblast (*mes*) entering by the choroidal fissure (Pl. IV. figs. 19, 20). Even in the later larval stages this complex anterior annulus, formed of the cells just mentioned, and the pigmented choroid which grows round to enclose a circular opening in front of the eye—the pupil, constitutes a brilliantly opalescent iris, which adds to the remarkable appearance of the minute transparent larva (Pl. XVI. figs. 3, 7, 9; Pl. XVIII. fig. 11).

Cranial Nerves.—The optic, olfactory, and auditory nerves are treated elsewhere, and in this place only the larger and more important nerve-origins will be referred to, the Teleostean embryo being little favourable for tracing the development of the smaller cranial nerves, such as III., IV., and VI. The trigeminal (V.) is large, and readily made out. In Elasmobranchs it arises as two lateral outgrowths from a median dorsal ridge at the anterior end of the hind-brain. At a late embryonic stage this nerve springs from the upper lateral margin of the hind-brain, but so far forward that the optic lobe covers it at this point, and it appears to emerge from the overlapping lobes at a point immediately posterior to the eyes. This lateral position must be secondary (as MARSHALL suggests in the case of *Scyllium*), the original median dorsal position being altered by the rapid growth of the roof of the brain, so that the origins of this pair of nerves become further and further separated, until finally they are lateral (No. 101). Just as the nerve emerges it separates into several rami, the outermost being the maxillo-palatine branch, while a second large branch, the mandibular, passes backward a short distance in close contact with the side of the medulla oblongata. Each of these main rami shows, near its origin, a very large ganglion, the two ganglia being so close together as to appear like slightly separated moieties of one primary ganglionic swelling. From the ganglion of the maxillary nerve a small nervous branch passes forward over the orbital arch, possibly the abducens (VI.), though more probably it is the ramus ophthalmicus of the VIth nerve. Between the two main rami just mentioned a large blood-vessel passes, and a third ganglion appears beneath it, also apparently one of the trigeminal group, while a slender nerve, whose destination could not be made out, was connected with this smaller ganglion. A little posterior to the trigeminal the VIIth and VIIIth arise in close proximity to each other, the auditory being posterior and exhibiting a large ganglion.

It is difficult to follow the fibres of two nerves, so contiguous, to their centres in the brain; but fibres can be traced from the upper lateral edge of the medulla over a wide curve which brings them near the base of the third ventricle, or more correctly above the pyramids; these must belong to the facialis; and the auditory (VIII.) consists of those fibres which come out close to the surface of the medulla just below the overlapping posterior part of the optic lobe. These two nerves, in regard to their nuclei, thus are widely separated; but where they arise from their common site on the upper margin of the medulla they are separable only by the fact that the fibres of the facialis pass down to the mandible and posterior margin of the hymandibular cartilage; while the VIIIth nerve has a very short course, breaking up on the under surface of the auditory sac to supply at least three special sensory areas (*neu*, Pl. VI. figs. 3, 4, 9, 10) in the otocystic chamber, and forming a prominent ganglion outside the ear before doing so. Of the glosso-pharyngeal nothing can be said here, but the vagus (X.) apparently arises by two complex roots; the first, which probably includes the fibres of the IXth nerve, issuing from a point near the lateral summit of the medulla oblongata, which point is in the same transverse plane as the oral termination of the notochord. It passes along the side of the medulla and penetrates the auditory cartilage, sending twigs apparently to the four gill-arches and to the pharynx. The nucleus of this portion of the vagus is confined to the superficial swelling of the lateral ridge of the medulla. Not so with the second part of the vagus. Its fibres describe an arch or curve, and can be traced to the median region of the medulla below the floor of the fourth ventricle and above the pyramids, while part of its fibres have a more superficial origin. On emerging they form a very massive, prominent root, passing in the main through the hind part of the ear-capsule, just above the thick basilar plate where it is in contact with the otocyst, and forming in front of the pectoral girdle a large double ganglion below and to some extent internal to the ear. The section which shows this bifid ganglionic mass presents another ganglion, apparently the ganglion of the first part of the complex. This ganglion is smaller, somewhat higher, and posterior to the large double ganglion. The former lies on the inner side of the anterior cardinal trunk, below which is a slender ganglion, whence twigs can be traced to the opercular region and to the skin, forming, between the muscle-plates and the neurodermis, a nervous tract, probably the origin of the lateral line.

The large double ganglion first named lies just above and external to the pronephric swelling, the intimate relation of the two structures being noteworthy. Its fibres go, as before said, to the pharynx and the branchial arches. From the smaller ganglion, described above, pharyngeal and important cardiac branches also pass.

Lateral Sense-Organs.—Little can be added to the observations of Hoffman (No. 69) with reference to the development of the lateral sense-organs. In a young gurnard, about eight days old, they are very distinctly seen in the transparent though somewhat corrugated and glandular integument. Generally three or four can be made out in the haddock, one on the top of the head, just behind the eyes, a second situated a short distance behind the pectoral fin (see Pl. XVII. fig. 1), while one or two occur along the caudal trunk.

They are not, however, regularly arranged, and the distal enlargement protruding from the integument is often absent. Thus, in the gurnard above referred to, nerve-filaments were observed passing across the sub-epidermal space from the trunk, and terminating in the skin without an enlarged sensory-organ. The external sensory-organ (Pl. VI. figs. 8, 8*a*) consists of a somewhat elliptical aggregation of granular columnar cells, from which a number of very fine and apparently rigidly erect palpocils (*plp*) project. A delicate nerve-filament (*nv*) passes from it to the muscular plates (*my*), and so to the central nervous system. This filament shows a slight enlargement at its proximal end, and another dilatation just as it approaches the external sensory-organ.

As noted on a previous page, large spaces (*ss*) filled with a clear plasma exist below the integument (*ep*), separating it widely from the trunk (Pl. XV. fig. 7), and across these spaces in more advanced embryos fine nervous threads pass from the myotomes to the skin, occasionally giving off in their course delicate secondary filaments. The nerve going to the cephalic sensory-organ apparently comes from a cutaneous sensory branch; and HOFFMAN states (No. 69) that the development of the ramus lateralis nervi vagi always precedes the appearance of these sensory-organs.

No sections of the early stages show the longitudinal sensory tract called the "lateral line" in fishes. There is, however, in the caudal trunk of an advanced haddock a canal apparently surrounded by nervous cells and mucous tissue which stains deeply (Pl. XI. fig. 16), but it can only be traced a short distance in the tail of the example referred to. As noticed elsewhere, the facial region is provided with numerous papilliform sensory bodies, and these are large and very noticeable in what may be called the maxillary or sub-prosencephalic region. They exhibit a structure similar to the lateral sensory-organs, and are composed of lengthened spindle-shaped cells (Pl. XXI. fig. 7, *sb*).

Alimentary Canal.—In its earliest condition the alimentary tract consists merely of a thickened sub-embryonic layer of hypoblast, intervening between the neurochord above and the yolk, or rather periblastic cortex of the yolk, below. Posteriorly, when little more than one-third of the yolk is covered by the blastoderm, the hypoblastic cells beneath the embryonic axis, as already pointed out, assume a distinct columnar character (*hy*); a lumen (*hg*) appears below, which is arched over by columnar hypoblast, and has a floor of nucleated periblast (*per*, Pl. IV. figs. 5*b*, 6). This is the first indication of the alimentary tube, and it forms the posterior section—the continuity of which with the neurenteric canal and medullary groove has been already described. From the arched enteric roof the notochord is differentiated. The lumen at first extends but a very short distance forward, and is lost in an anterior aggregation of hypoblastic cells. These cells, formed by the proliferation of the thin sheet of invaginated hypoblast, reach as far as the cardiac region, where they thin out rapidly, and form a delicate limiting membrane below the head (*hy*, Pl. IV. figs. 3, 4). As this thickened mesenteric mass arises, the embryo is necessarily raised from the yolk except in the cephalic region—the snout still lying in close contact with the yolk below, so that a pseudo-cranial flexure is produced, and a pericardial space (*pd*) formed beneath the otocystic region

At the sides of this space, *i.e.*, beneath the eyes, the hypoblast becomes thickened as two lateral longitudinal ridges (Pl. IX. fig. 1; Pl. XI. fig. 1), but elsewhere in this region the layer forms a very thin plate (Pl. IV. fig. 21). That the roof of the primitive enteron is thus formed as a dorsal sheet of invaginated hypoblast, admits of no doubt. Such sections as figs. 5*b*, 6, and 10, Pl. IV., demonstrate this, and the ventral wall of the canal is formed of cells either pushed in from the side—that is, formed of true hypoblastic cells or aggregated as masses of protoplasm around the scattered nuclei of the periblast, and budded off. While the posterior portion is formed in this way, the mesenteron proper appears to develop in a different manner, being formed by a multiplication of the invaginated (hypoblastic) cells; and a ventral and a dorsal wall are not definitely formed from periblastic and hypoblastic cells respectively, but doubtless periblastic cells contribute in some degree to build up this portion of the tract also, though in such sections as figs. 13 and 14, Pl. IV., the hypoblast (*hy*) is a very definite and continuous layer. The mid and fore portions form a dense cord, in which a lumen appears later by the forward extension of the posterior enteric chamber, this œsophageal slit extending in the ling, two days old, in front of the otocystic region. At first the hind gut is open to the yolk below (as in Pl. IV. figs. 5*b*, 6), but no sections show this to be true of the enteric tract further forward. According to Hoffman, paired involutions of hypoblast produce the tract which he thus holds to be open to the yolk beneath (*vide* No. 69*a*, Taf. i. fig. 3), but no section in pelagic forms indicates such a mode of origin of the mesenteron, and certainly not of its œsophageal portion. The earliest condition of the alimentary tract is a continuous sheet of hypoblast, thickened on each side in the oral region to form the lateral walls of the oral chamber. Lereboullet regards the alimentary canal as developed by a folding-in of the "mucous layer," though the pharyngeal section, he holds, is not formed till later. In his earlier researches he states that the enteric tract is possibly formed by "une végétation celluleuse," such as Vogt had described as involved in the formation, not only of the intestinal tube, but of the liver and kidneys (No. 93, p. 538). Dohrn believes that the oral hypoblast is a forward growth of the mesenteric mass, nor is there evidence to show that this is not so. At any rate, in the embryo whose optic vesicles are in process of formation, the hypoblast (*hy*, Pl. IV. figs. 4, 13, 14, 20) is a thin sheet—a single layer of cells for the most part over the entire ventral surface, save at the posterior extremity (*hy*, Pl. IV. fig. 10). At a somewhat later date, when the invagination of the lenses is completed, the mesenteron is a massive cylinder, and the oral tract a wide flattened sheet of hypoblast formed either by proliferation of the invaginated layer, or by forward growth of the denser hind gut, probably a combination of both. In any case, Lereboullet's view is the correct one, viz., that the pharynx is a separate and later formation than the mesenteron proper. By the time the walls of the otocysts have thinned out and their chamber has enlarged and contains the otoliths, a fine horizontal fissure traverses the pharynx, and a lumen thus continues from the oral to the blind anal end of the alimentary canal (Pl. IV. fig. 11). The cells now assume the full cubical columnar character characteristic of the enteric epithelium, and, at first a single layer

(Pl. IV. figs. 11, 19), they increase until the enteric walls are thick, and include many layers of wedge-shaped cells (Pl. VII. figs. 7, 9). In *P. flesus* of the ninth day (*i.e.*, two days before hatching) the walls are just ·001 inch in thickness, and the lumen in the middle or widest part measures in horizontal breadth slightly less. A delicate inner layer lines the lumen, which has a granular or mucoid appearance, but it subsequently forms a ciliated enteric lining. It is not more than ·000125 inch in thickness. The lumen of the mid gut is large and round in transverse section (*mg*, Pl. VII. fig. 3), but much more depressed further forward. A section through the pectoral region, where the enteron is oval and the lumen a wide transverse fissure, shows a diminished dorso-ventral capacity, while in the oral region proper a mere horizontal slit extends from side to side of the wide and very much depressed layer of œsophageal hypoblast (Pl. XI. figs. 2–8). The tract is thus a closed sac (Pl. IV. fig. 12), flattened anteriorly, round and cylindrical posteriorly, the mouth and anus being "the last parts," as LEREBOULLET said, "to be formed." Around this tube of hypoblastic cells the splanchnopleure (*sp*) grows, forming a thin external sheet which pushes in below the notochord, and cuts off that structure from the mesenteron (Pl. VII. fig. 6). These mesoblastic cells do not become a fibrous layer for some time, but later they give origin to the muscles of the canal and its connective-tissue, while externally they give rise to the epithelial peritoneal layer.

In the œsophageal region the course of the hypoblastic cells is extremely difficult to follow. They give origin to a cardiac swelling which is sub-oral and median (*hr*, Pl. IV. fig. 13; Pl. V. fig. 8), while other cells pass into the hypoblast laterally to form the core of the visceral folds. During the first few days after hatching the anus is still undifferentiated, as LEREBOULLET found to be the case in *Perca;* nor is the oral cavity externally open, as the same observer also proved in *Perca* by experiments with various colouring matters (*e.g.*, indigo), the alimentary tract being in fact a closed cylinder, consisting of a very thick inner wall of cylindrical cells (*hy*, Pl. IV. fig. 11), whose free rounded ends project into the cavity of the gut (*fg*), and externally of a thin layer of flattened mesoblastic cells (*sp*) not yet transformed into muscular and other tissues (*vide* No. 93, p. 625).

Many preparations show a lining apparently of cilia,* and there is thus great probability that the enteric tract—the œsophageal portion at least—of young Teleosteans is ciliated. Its walls for some time are straight and smooth, but in later stages folds and wrinkles are formed, the intestine especially showing a complexly folded internal surface (Pl. XIV. fig. 5; Pl. XVIII. figs. 1, 11). The various parts of the tract become rudely marked during the first week after hatching. Thus a gurnard on the thirteenth day (Pl. VII. fig. 9) shows very distinctly a capacious though depressed oral chamber, the floor of which is ridged by the branchial bars and hyoidean framework, followed by a wide œsophagus (*fg*), the lumen of which is so flattened as to be little more than a horizontal fissure in transverse section. From this portion the duct of the swim-bladder passes (Pl. VII. fig. 4).† The enlarged

* SHIPLEY has recently described the œsophagus in *Petromyzon* (47th day) as ciliated (No. 150, p. 351).

† *Vide* the highly suggestive remarks of Prof. CLELAND on Teleostean pneumatic ducts—*Memoirs, &c., in Anatomy*, 1889, p. 170.

stomach (*st*) follows, and beneath its thin walls the hepatic mass lies. A fourth portion of the tract succeeds, viz., the pyloric section, the dense walls of which give origin to those remarkable diverticula, the pyloric cœca. These seem to be merely blind evaginations, and gradually assume a lanceolate form, as we find in young cod from $\frac{1}{4}$ to $1\frac{1}{2}$ inch in length. Ventrally a well-marked duct passes from the liver, viz., the ductus choledochus, with several ramose biliary ducts. The intestinal walls are very dense, rapidly develop a glandular character, and have a narrow oval lumen (*hg*) with local enlargements, especially in the mid portion of the gut. Posteriorly it narrows again until the rectal region is reached, where a cincture or valve occurs, behind which its capacity once more enlarges (see also *hg*, fig. 8 on the same plate); it then bends downward, and narrows to form the small anal aperture (*a*) opening upon a muscular papilla. A similar condition of the intestine and rectum is seen in the figure of *P. platessa* (Pl. XIV. fig. 5). The rugose walls often exhibit vermicular movements, which are, however, very irregular, and involve and produce great contortions in the alimentary tract; thus a peristaltic motion may pass from the mesenteron to the rectum, narrowing its capacity as though by an embracing cincture.

Mouth.—A stomodæum or involution of epiblast to form the mouth is never really formed in pelagic Teleosteans.* The oral cavity is capacious, and the branchial framework supporting its floor and sides is fairly advanced when a fine transverse fissure is seen passing across the under surface of the head below the eyes (*m*, Pl. IX. fig. 2). This fissure enlarges and lengthens, forming an almond-shaped opening (*m*, Pl. IX. fig. 3) across the subcephalic membrane. This is the mouth, and it is formed as a slit by the lumen of the buccal chamber bursting through. Its edges are jagged, and strands of cellular tissue often pass across from one lip to the other one or two days after the oral opening appears (Pl. IX. fig. 3), showing that it is an actual severance of a complete epiblastic membrane. There is no indication of the double origin, the coalescence of two lateral clefts which Dohrn has described in *Gobius*, *Belone*, and *Hippocampus* (No. 52*a*); but in the ling—the species illustrated in the figures just referred to, and in other forms—this median transverse fissure suddenly appears, and in the course of two or three days widens antero-posteriorly to form a large median tubular opening.† The lips do not move, but the hyoid cartilages are flexible and mobile, and the floor of the mouth is thus raised and depressed. The mandibular cartilages rapidly grow forward, and the oral opening—at first ventral, transverse, and shark-like—assumes the shape found in the adult Teleostean, the prolongation of the mandible not only bringing forward the aperture of the mouth (Pl. XII. figs. 2, 6, 7), but proceeding so fast and to such a degree that the floor actually extends beyond the snout, and the aperture now opens from above (Pl. X. figs. 1, 2, 3, 5, 5*a*). The suborbital curtains, which hang down like two membranous flaps, diminish, and become denser on account of the development in their tissue of maxillary bars, the chitinous character and form of which are elsewhere described.

* Parker describes a true stomodæum in the salmon, but probably his account of the ingrowth of epiblast to form the mucous membrane of the mouth and fauces requires confirmation.

† Dohrn, on the contrary, describes the centre of the oral slit as still closed when the lateral portions have broken through.

Anus.—The anus in the forms here described is not a proctodæum, as it is not produced by the ingrowth of the external epiblast, but is at first a lateral opening (see Pl. VII. figs. 12–15), which five or six days after hatching is formed by the protrusion of the anal section of the alimentary canal. In *Molva vulgaris*, early on the second day after emerging, the anal tract seems still to end blindly, being continued backward nearly in a straight line, or in some cases sending down a terminal process at right angles to the main axis of the canal. This terminal prolongation is carried down to the middle of the marginal fin, and generally on the second or third day is found to break through in a manner not unlike the oral opening. The rectum is thus a capacious thick-walled tube, sending out a narrow anal continuation consisting of a fine tube lined by a single layer of cubical epithelium, and it passes through the thick tenacious plasma contained in the space behind the urinary vesicle (Pl. VII. figs. 12, 13). This space is enclosed between the two epiblastic lamellæ of the caudal membrane, and the anal tube curves round and opens laterally on the surface of the latter, some distance from the ventral margin. Later the membrane below the aperture becomes absorbed, the rectum assumes thicker walls (*hg*, Pl. VII. figs. 8, 9), and the usual muscular rectal portion of the alimentary canal is formed during the second week after emerging. The anus then opens in the ventral middle line, as in the adult fish.

Liver.—Soon after the otocysts are formed the ventral wall of the mesenteron in its fore part shows an enlargement—"an ovoid dilatation just before and below the early pectorals," according to Lereboullet (No. 93, p. 584), and his description holds to a large degree for pelagic Teleosteans. Certainly the liver is a distinct outgrowth from the ventral wall of the mesenteron. Hoffman has expressed the view that the liver originates from the yolk-periblast, and that the hepatic diverticulum is really a proliferation of "parablast entoderm" (No. 69*a*). Such sections as fig. 2, Pl. VII., do not support this view, for the periblast (*per*) is a distinct, granular layer beneath, and separated by a delicate stratum of hypoblast (*hy*) from the cells which build up the liver. The liver, in fact, is largely a solid proliferation of the ventral wall of the mesenteron, and is periblastic, or formed of "parablast entoderm" only in the degree that the ventral wall of this region is periblastic, and this we have seen at this point to be at a minimum. Into the early liver (*lr*, Pl. VII. fig. 5) a delicate canal (*dc*) passes, a direct prolongation of the enteric lumen, doubtless the ductus choledochus. Lereboullet noticed this especially when the mesenteron dilated and contracted as it does in later embryonic stages (No. 93, p. 593). In *Perca*, on the sixth day, the same observer describes numerous ramifying fissures or prolongations from this delicate canal; and the gall-bladder he regards also as a tubular outgrowth of the intestine. The hepatic proliferation becomes bifid, a dorsal and a sinistral ventral lobe being distinguishable. The liver also becomes divided into small lobuli (*lr*, Pl. VII. figs. 1–3), in the midst of which the spacious gall-bladder (*gb*) appears as a clear vesicle, limited by an epithelial wall of a single layer of cells.

Swim-Bladder.—From the dorsal wall of the mesenteron (*mg*) the swim-bladder (*sb*)

is given off as a very thick-walled diverticulum (Pl. VII. fig. 5), which presses upwards against the notochord, and remains connected for some time by a fine canal (Pl. VII. figs. 2, 4). Before the embryonic period ends, however, the duct atrophies, all the forms specially referred to being physoclistous.

Heart and Circulation.—The heart is developed at a very early stage—before the œsophagus is formed—as a cylindrical structure (*hr*, Pl. IV. figs. 8, 12), in front of the pectoral region, *i.e.*, between the otocysts and the optic vesicles. Soon after the alimentary tract is defined, or, as Wenckebach expresses it (in the case of *Belone*), after the ventral closure of the gut, and when about twenty-four proto-vertebræ are marked off, the heart has a vermiform shape, and is still solid. This solid condition Lereboullet described in *Perca*, but in *Salmo* and other forms the heart is stated to appear in the form of a single or double tube (*vide* Hoffman, No. 69*a*; Balfour, No. 11, p. 637). That the heart develops as a single tube in the Gadoid and other forms here considered is not surprising. When the heart arises as two tubes it appears to be connected, as Balfour pointed out (No. 15, vol. xi. p. 689), with the non-closure of the pharynx inferiorly, but in those Teleosteans where the œsophageal cavity is formed later by a forward growth of the enteric lumen, the solid tract is really closed below, and this is the condition correlated with an unpaired cardiac rudiment. Its first indication in the living embryo is seen as a rounded projection beneath the solid œsophagus bulging out towards the subjacent periblast. It is a ventral outgrowth of that splanchnic mesoblast, which also forms the branchial arches. Lereboullet describes this cardiac swelling (on the seventh day in *Perca*) as having its inferior portion, the auricle, resting directly on the yolk (No. 93, p. 584; *vide* his pl. iii. fig. 13). It is a median unpaired projection, and carries down before it a very thin layer of hypoblast. At times this delicate stratum of hypoblast cannot be made out, and in *P. platessa* it would appear to be absent; nor can a layer of hypoblast be distinguished over the rest of the surface of the yolk, though such a layer is readily seen in other Pleuronectids, as well as in Gadoids (Pl. VIII. fig. 11). In all cases, however, the continuity of the rudimentary heart and the "branchial" mesoblast above is maintained.* Hoffman describes in *Salmo* two lateral folds of splanchnic mesoblast, which pass down beneath the pharynx, and produce by a dorsal and a ventral union a tubular heart (No. 69*a*; *vide* fig. 9, Taf. ii.). Before the tube is complete inferiorly, some intruding cells of "parablastic entoderm," *i.e.*, periblast, form the cardiac endothelium (No. 69*a*, Taf. iii. fig. 6; Taf. iv. fig. 6). Such a process does not accord with the appearance of the heart in the living condition, for in the embryonic cod, haddock, and others no lumen is visible at first, as Oellacher and Gotte also hold, and indeed after the lumen is formed the endothelial lining is absent (*vide* surface-views, Pl. VIII. figs. 3, 7; and

* Wenckebach (*op. cit.*, and *Jour. Roy. Micr. Soc.*, February 1887) describes its first appearance as a band of mesodermic cells close behind the optic vesicle on the lower surface. They arise from the indifferent mesodermic cells of the head which wander round the gut. The mass of cells splits to form a kind of pouch—the heart. The blood-vessels have a similar mesodermic origin. The heart opens into the segmentation-cavity, and its lumen is nothing else than part of the blastocœl. The blood is mesodermic in origin, he avers, neither endoderm nor free periblast, *i.e.*, nuclei, having any share in its formation.

sections, Pl. XI. figs. 2, 3), indicating that the epithelioid layer is not formed in some Teleosteans simultaneously with the formation of the cardiac tube, and favouring the view that the heart becomes tubular by dehiscence of its median cells, or, as LEREBOULLET says, the linear cavity is formed partly by separation of cells and partly by absorption (No. 93, p. 551).* It seems probable that in different Teleosteans this organ has a different structure primarily, and certainly at later stages the circulatory system diverges in various species. Thus in the Gadoids, Pleuronectids, *Trigla*, and other pelagic forms, no yolk-circulation is ever developed, whereas in most demersal forms a circulation upon the surface of the yolk is a very striking feature, and may be said to a certain extent to precede the heart's action; for TRUMAN found in *Esox* that blood-corpuscles were formed in patches in the cortex of the yolk, constituting the "islands of blood-corpuscles" which GENSCH has described (No. 56), and that before the heart pulsates, blood actually moves towards that organ. At the eighty-sixth hour TRUMAN saw these moving corpuscles reach the heart, but it was ten or twelve hours later before the organ exhibited any motion, and even then no corpuscles passed into its cavity (No. 154, p. 191); so that the pulsations are independent of any stimulus given by the presence of blood-corpuscles within its chambers. Muscular twitchings, again, are often observed in the heart of the gurnard before the proper pulsations begin. We have already seen that the cardiac chamber is enlarged by the raising of the head of the embryo, and LEREBOULLET noticed that as this took place in *Perca* the heart becomes detached from the head, its anterior end following the retreat of the yolk, sinking slowly, while the hind end remains attached under the embryo. While yet a simple tube, the heart is contractile, the early pulsations, which commence usually one or two days after the heart is formed, being one of the most noteworthy features in the developing embryo, though no hæmal fluid can be made out.† At first the pulsations are very slow and intermittent, the intervals between the contractions being irregular. In an embryo, four days after fertilisation, the beats are more rapid and regular, averaging 48 pulsations per minute, while the rate at times is greatly increased. Thus Dr TRUMAN found in *Esox*, soon after the heart began to beat (at the ninety-ninth hour), they reached 104 per minute (No. 154, p. 193), but the conditions must have been abnormal. The rate noted by LEREBOULLET in *Perca*, viz., 40, 50, or 60 times per minute, is normal (No. 93, p. 451). In a ling of the second day (Pl. XIII. fig. 4) the pulsations were observed to have reached the rate of 80 beats per minute. The endothelial lining of the heart appears as a single delicate layer of cells, very much flattened and loosely suspended in the cardiac chamber, apparently derived from the myocardium or thick contractile layer. OELLACHER regards it as developed in the trout from the hypoblast beneath, and his figures on Taf. iv. (No. 114) are very clear; but no such continuity of the endocardium with the limiting hypoblast below is shown in

* In certain insects PATTEN has found that two mesodermic plates by a median longitudinal fusion form a solid cord (*Phryganida*), while in others (*Blatta*) it is hollow from the time of its formation, and the mesodermic folds pulsate long before they unite to form the heart (PATTEN, "Develop. of Phryganids," *Quart. Jour. Micr. Sci.*, vol. xxiv., 1884, pp. 587, 597).

† *Trawling Report*, 1884.

sections of our forms. Certainly it is not formed, as has been suggested for the chick, by wandering corpuscles from the area vasculosa, which, finding access to the heart, cling to its walls as a loose lining, for in Teleosteans this endocardium is present before the hæmal circulation is in action. HOFFMAN's figures (No. 69*a*, Taf. iii. fig. 9, Taf. iv. fig. 6) do not represent the primary condition in our forms, for the heart usually pushes down before it a delicate stratum of hypoblastic cells (*hyp*, Pl. VIII. fig. 11; Pl. XI. fig. 2); but this limiting ventral layer apparently becomes obliterated anteriorly, and the pericardial chamber is open to the subembryonic space, which is undoubtedly the persisting germinal cavity. The vermiform outline (*h*, Pl. VIII. fig. 3; Pl. XII. fig. 4) soon undergoes modification, and the posterior end becomes expanded, while the anterior and upper ventricular portion remains narrow (*h*, Pl. XIV. fig. 1). Thus the simple cardiac tube becomes cone-shaped, the apex of the cone being continuous with the sub-œsophageal mesoblast (*mes*, Pl. VIII. fig. 11), while the lower anterior end is comparatively free, though not perfectly so, as a thin mesoblastic membrane (Pl. VIII. fig. 5) continuous with the free edge of the auricle separates the myocardium from the exterior, and a space is formed—the pericardial chamber (*pd*) around the heart.

By its mode of formation as a downward growth the heart has at first a somewhat vertical position; but with its increase in length it extends further and further forward beneath the head, and moreover it becomes flexed to the right (Pl. VIII. figs. 2, 9). The anterior position of the heart at this time is quite characteristic of the early embryo. The before-mentioned delicate pericardial walls are involved in the rhythmic movements of the organ, and sway to and fro with each systole and diastole.

The splanchnic mesoblast, out of which the heart and pericardium are formed, has relations similar to the splanchnopleuric prolongation in the region of the trunk proper, —the pericardial cavity surrounding the heart just as the cœloma encloses the abdominal viscera,—the view that the former is merely a part separated off from the latter by the posterior (pericardial) septum being strikingly supported by the condition in the Cyclostomes, in which an intercommunication of pericardium and body-cavity persists throughout life.

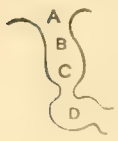
The first change in the position of the slightly curved cylindrical heart (Pl. VIII. fig. 5) results in its assuming an L-shaped form (as in Pl. IX. fig. 1, *h*), the small arterial end (ventricle, *ven*) still occupying the median position, while the auricular end (*aur*) is turned at right angles. In the figure before referred to, the flexure is still more apparent; while in fig. 3, Pl. XII., the auricle, previously directed to the front (Pl. VIII. figs. 3, 6, 8), is now posterior (see also Pl. VIII. fig. 9), the flexure continuing to increase as development proceeds. Thus the relations of the auricle and ventricle are reversed, and the latter, which is now anterior, becomes bulbous (*ven*, Pl. VIII. fig. 7), and distinctly marked off by a constriction; while the auricle (*au*) itself is separated by a cincture into auricle proper and sinus venosus (*sv*). The blind continuation of the ventricle into the subpharyngeal mesoblast (*mes*, Pl. VIII. fig. 11) above is really the rudimentary bulbus arteriosus, so that the four parts may be distinguished, as RYDER pointed out (No. 141,

p. 537), about or soon after the time of hatching. Occasionally one or more detached cells may be seen loosely suspended in the auricle, near its external opening, and they swing to and fro with the heart's pulsations. No blood, as such, exists until a later stage, and any fluid included in the lumen of the heart and the pericardium must be non-corpusculated, and its presence cannot be demonstrated. It may be doubted whether the stray corpuscles above referred to are blood-elements at all, for LEREBOULLET is almost certainly correct when he says that it is erroneous to assert that the corpuscles which first appear in the heart are detached from its walls: "they are different in character, and too coherent to become detached" (No. 93, p. 585). In our specimens these had the appearance of papillæ on the cardiac wall. RYDER regards the periblast as the source of the blood-corpuscles, in accordance with HOFFMAN (*Zool. Anz.*, 1880, p. 633); and in this view their connection with the so-called free nuclei around and beneath the early blastoderm is naturally suggested. RYDER contends (No. 141, p. 537) that the pericardial cavity is really the persisting segmentation- (or more correctly, germinal) cavity, and that the passage of periblastic blood-elements into the heart is thus secured. It must be remembered, however, that the roof of the germinal cavity consists of the subembryonic hypoblast, a layer which stretches beyond the tip of the snout of the young fish, and extends as the under-stratum of the double-layered yolk-sac (*ys*, Pl. V. fig. 8). This subcephalic chamber, with its floor of periblast and roof of hypoblast, is never obliterated; but though its periblastic floor does not bud off cells to form the ventral half of the mesenteric wall, yet its roof (*ys*) becomes pushed downward (*vide* Pl. XII. figs. 1, 3) until it lies below the pericardium (Pl. XII. fig. 2; also see Pl. VIII. fig. 6), and is separated only by a narrow fissure from the periblast (*per*) beneath. The germinal cavity diminishes in a less degree laterally, and the latero-pharyngeal spaces into which the embryonic breathing aperture opens from without (see p. 747) are its more visible remnants (*ss*, Pl. IV. fig. 21; Pl. XI. figs. 6, 7, 8). The floor of the pericardium appears (*vide* Pl. IV. fig. 21) to be obliterated anteriorly, but even in this case the delicate hypoblast would seem still to separate the pericardial from the germinal cavity below. The absence of the limiting layer from a certain area may be explained also, not by obliteration, but by a different method of origin, and it is quite possible that the pericardium may be a fold of mesoblast directed forward. TRUMAN, indeed, speaks of such a mode of development in *Esox*, a membranous fold being reflected from the under part of the head (No. 154, p. 190).

Meanwhile the vascular canals of the trunk are in course of formation, a small arterial vessel (the dorsal aorta) being hollowed out of the loose trabecular tissue (really the intruding mesoblastic cells above the gut which are broken down) along the under side of the notochord (*x*, Pl. VII. figs. 1, 4, 6; Pl. XII. fig. 8), and two venous trunks of large calibre are similarly formed in the lateral connective tissue just external to each head-kidney. In the living larva of *Molva vulgaris*, on the fourth day, the subnotochordal tissue seems to be traversed by a single large vascular channel (*vn*) separated by an interval, probably the dorsal aorta (*ao*), from the chorda (*nc*). The large channel can

be traced from the liver posteriorly to the caudal region, and it contains numerous large round corpuscles, though these do not seem to occur anterior to the liver (Pl. XV. fig. 1). Again the venous trunks immediately in front of the pectoral fins send prolongations downward, and communicate with the venous end of the heart, which at this time shows the broad auricle directed upward and backward, and a spacious sinus venosus (*sv*, Pl. XII. fig. 8). The large venous tube thus passing to the sinus on each side is the ductus Cuvieri, which, in addition to the posterior (cardinal) vein, also receives the anterior (jugular) trunk. Around the two anterior veins the cellular tissue of the pronephros grows (*prn*, Pl. XI. figs. 9, 11), and venous ramifications are developed in the midst of the renal matrix. Before the end of the first week after hatching—generally on the fourth or fifth day in Gadoids—a simple circulation can be detected. The anterior bulbous end of the heart driving the blood upwards behind the eyes—probably by the artery of the hyoid arch, whence it courses by the great subnotochordal trunk (dorsal aorta) to a point a little posterior to the root of the tail, and, passing round by a minute loop, returns by a large venous trunk which anteriorly divides into the two cardinals already mentioned. The two subnotochordal trunks with the anterior branchial artery constitute the simple vascular system in its earliest condition. A day or two later a venous branch leaves the vena vertebralis at a point about midway along the trunk—above the mesenteron, and passes down to the lower side of the alimentary canal—and forward along the margin of the liver to the sinus venosus. This must be the subintestinal vein, which is, however, usually described as passing along the intestinal portion of the alimentary canal. Its course, however, is at this stage very short. Not so in the case of the intestinal artery (cœliaco-mesenteric) which leaves the dorsal aorta in the pectoral region, traverses the mesenteron in descending, then courses beneath the rectum, but ascends before reaching the anus, and passes along the anterior margin of the urinary vesicle to join the caudal vein. The caudal vein is lengthening simultaneously with the caudal artery; thus, in a cod on the seventh day both reached barely a quarter the length of the caudal trunk, while on the fourteenth day they extended almost to the tip of the tail. The force of the arterial current seems to hollow out the yielding channel, and causes it to become longer, but the afferent venous trunk has the appearance of a somewhat irregular ill-defined sinus. During the second week great advances take place in the hæmal circulation. Lereboullet noticed, in *Perca* about two weeks old, that blood was passing along two of the gill-arches; and in the Gadoids and other forms described in this paper two arches likewise develop arterial channels. There is considerable variation in the details of this development; thus a haddock, on the fourteenth day after extrusion, showed arterial blood passing along two (apparently the anterior) branchial arches, whereas another embryo of the same species, on the eleventh day, showed three branchial arteries and a fourth artery, which runs apparently within the opercular fold, possibly, however, the hyo-opercular. The mandibular artery is a well-marked trunk coursing along the outer margin of the

mandible.* Both arteries meet in front of the symphysis, and return by a single median vein along the floor of the mouth. The later developments of the hæmal system at a stage—in, say, *Gadus morrhua*—when the caudal artery extends along fully two-thirds the length of the tail, are as follow:—Four branchial arteries can be made out, and a submaxillary artery passes beneath the eyes, while a return-current is directed over the eyes, along the supraocular vein. The cœliac artery, before described as leaving the aorta in the pectoral region, passes over the liver, along the ventral surface of the intestine, and sends an arterial branch upward, which, bifurcating, supplies the walls of the intestine,—the main trunk continuing its ventral course, and ascending in front of the urinary vesicle,—over the walls of which it passes to the vena vertebralis. The venous trunks form a more complex system—the simple subintestinal loop which breaks up into an elaborate hepatic capillary network still continues, but it is joined by a large visceral trunk on the posterior side of the liver. This latter vessel leaves the caudal vein at the root of the tail, passes ventrally in front of the urinary vesicle and over the walls of the rectal portion of the intestine to the termination of the mid gut. At this point a large venous trunk branches off dorsally to join the posterior cardinals. Minor venous branches run from the walls of the stomach and pyloric portion of the intestine, forming the first indication of the portal system—all their blood finally passing in front of the liver into the sinus venosus by the hepatic veins. The liver, the dorsal lobe of which lies above the alimentary canal and behind the swim-bladder, is seen chiefly as a rounded mass (the left and ventral lobe) projecting boldly into the surface of the yolk below, and lying immediately in contact with the posterior pericardial wall. The proximity of the liver with its rich vascular plexus, and of the large ductus Cuvieri pouring a stream into the capacious sinus, suggest the possibility that it is at this point that the assimilation of yolk-matter is most active. It is absorbed and conveyed to the heart by the venous blood. The continuity of the wall, limiting the pericardial chamber (*pd*, Pl. VII. fig. 9), appears to be unbroken, and roofs over a sub-pericardial space (*ss*) filled with a serous plasma and disintegrated yolk. A suboral chamber in many cases seems also to be shut off by this membrane (Pl. VIII. figs. 6, 7). The heart's pulsations partake of a progressive vermiform movement, the auricle, continuous with the sinus venosus, contracting first, and the successive parts (of the auricle) contract in order, the ventricle dilating as the last part of the auricle closes. As the ventricle contracts, the open end of the auricle dilates.



The progressive systole being triple, . . 1 2 3

(See accompanying diagram,) . . . (A)—(B)—(C, D) contract / dilates

The diastole also is threefold, and D contracts simultaneously with the dilatation of A, . } (A)—(B)—(C) dilate / (D) contracts.

The delicate pelagic forms chiefly considered in these pages present a great contrast to

* Götte is certainly incorrect, as Balfour pointed out (No. 11, p. 645), in denying that a mandibular artery is ever developed in *Teleostei* (No. 59).

the stronger and more robust Teleosteans, which are at a very early stage, often long before extrusion from the egg, provided with a complex vitelline circulation. In such forms as *Salmo* (Pl. XXII. figs. 4–9), *Anarrhichas* (Pl. XX. figs. 2, 4, 5), *Gastrosteus*, *Cottus*, *Liparis* (Pl. XV. fig. 2), and *Cyclopterus*, the blood-corpuscles seem to be mainly derived from the nucleated particles into which the surface of the yolk becomes broken up, and, as already noted, TRUMAN found in *Esox* that hæmal channels appeared upon the yolk, and corpuscles slowly moved towards the heart before this organ showed any motion. No such blood-canals are excavated in the yolk of the pelagic forms here treated of, indeed no yolk-circulation ever truly exists in the gurnard, cod, and allied forms. Nevertheless, the yolk steadily diminishes, and in embryos, fourteen to twenty days after hatching, it forms but a very slight projection, and at the end of the first month would appear to be entirely absorbed (compare fig. 5, Pl. XIX. and fig. 1, Pl. XVI.). The surface of the yolk, however, shows during this time rapid disintegration (*vide* Pl. VII. fig. 9), vesicles, granules, and nucleated particles appear in it (Pl. XI. fig. 12), and are especially noticeable around the large oleaginous spheres (Pl. XI. fig. 13) in those forms, such as the gurnard, ling, and others, in which these striking bodies occur. The protoplasmic envelope of the globule in such cases becomes richly provided with large nuclei showing one or more nucleoli, and similar bodies occur superficially over the yolk. In a young perch, eleven to fourteen days old, LEREBOULLET observed, just as we have noticed in the Gadoids and other forms, the dorsal aorta, formed by the union of the vessels of the branchial arches, sending a supply to the intestine and adjacent viscera, and reaching to the extremity of the tail, while of venous trunks the two anterior and two posterior cardinals and the subintestinal vein are common to both. In *Perca*, in addition to the above trunks—developed no doubt in all Teleostean larvæ, a complex yolk-circulation arises, and is supplied by branches from the posterior cardinals and from the subintestinal vein. These branches pass over the yolk as simple undulating lacunæ formed by the separation of the substance of the yolk-cortex, and meet on the ventral side of the yolk in a pair of large veins, which form one large sinus, continuous with the sinus venosus in the pericardial chamber. LEREBOULLET says of these vitelline vessels, that they do not appear to have proper walls, and form an ill-defined and irregular network; but on the third or fourth day after hatching the hæmal canals acquire definite walls, the network elongates, so that the main trunks show a parallel arrangement (No. 93, p. 601). In *Perca* the development of this circulation over the yolk is much more rapid than in *Esox*, and LEREBOULLET connects this with the larger perivitelline space in *Perca*, as there is a greater need for respiration; and for this reason, he says, in that species "the capsule is spacious, and holds so large a quantity of water" (No. 93, p. 610). The true explanation, however, seems to be that the more complex and rapid the circulation the more speedily the bulk of the yolk is reduced, and hence a large perivitelline space is produced. It is remarkable, however, that in such forms as the gurnard, rockling, the flat fishes, and Gadoids, in which no vitelline circulation ever develops, the yolk should still show a very rapid disintegration (compare Pl. XII. figs. 1 and 3, with Pl. X.

figs. 1, 2, and 3, and Pl. XVII. fig. 2). This does not take place, however, to any very appreciable extent while the embryo is within the ovum, whereas the reduction is very marked in *Perca* (No. 93, p. 610), *Cyclopterus*, and similar species. After the embryo emerges in pelagic forms, and before any circulation of a corpusculated hæmal fluid exists, the yolk, which is very large and prominent in the newly hatched fish, becomes speedily diminished. A process of absorption must be actively going on in these forms (*e.g.*, cod), and the presence of a transparent plasma bathing the tissues, and filling the pulsating heart and lacunæ of the trunk, is suggested.

The origin of the blood-corpuscles is an interesting point; but there is little unanimity amongst observers on this matter respecting Teleosteans, and appearances seem to support more than one suggested mode of origin. Ryder, with Hoffman and others, as we have already said, holds "that the blood-cells are budded off directly" from the periblast, the nuclei of which layer by division give rise to groups of granules, the form-elements of the blood (No. 141, p. 543). C. Vogt in 1842 distinguished a "couche hæmatogéne" (No. 155), as did also Rathke and Von Baer, their third or vascular layer of the blastoderm being, however, derived from the "lower layer" or hypoblast-cells; and Van Bambeke, while admitting that the periblast or "intermediary layer" has not been proved to be this "vascular layer," appears to consider their homology very probable (No. 20*a*, p. 9). Gensch's researches support this view, the corpuscles arising from the layer surrounding the yolk—"Kupffer's secondary entoderm." In opposition to Kupffer's affirmation that the outer mesodermal yolk-sac gives origin to the corpuscles, Gensch found that in *Esox* and *Zoarces viviparus* no mesoblast was present in the region where they arose, the two-layered epiblast lying upon the granular periblast in which cells were imbedded. These cells give out pseudopodial processes, which are constricted off to form corpuscles, and these by subdivision produce blood-islands (*vide* No. 56). In *Salmo*, *Alosa* (No. 141, p. 537), *Gastrosteus* (No. 122, p. 494), and other forms, the phenomenon described by Gensch has been observed, yet it is not conclusive that the primary corpuscles are derived from the "Dottersack." That the periblast contributes to the nutrient hæmal fluid of the embryo there can be no question, but the point of chief moment is, whence are the primary corpuscles derived? As Lereboullet long ago pointed out, the heart beats for some time before corpuscles appear in its lumen; and he added that the hæmal trunks too are formed, as in the gurnard, before the corpuscles (No. 93, p. 577). Wenckebach, however, holds that in the process of formation the blood-vessels give origin to the corpuscles, so that both originate contemporaneously. This observer concludes that the blood-corpuscles appear to him to arise in a solid mass of tissue in the region where the vena vertebralis is afterwards situated, the cells constituting this mass being carried away by a hæmal plasma, and acquire the colour and character of blood-corpuscles subsequently (No. 157). The polyhedral cells which Wenckebach shows filling up the lumen of the subnotochordal vein (*vide* No. 157, pl. viii. figs. 2, 3, &c.) are also found, in section, to fill up the aortic trunk, and there is no reason why the derivation of these blood-cells should not be extended to all the

hæmal vessels. The fact, however, seems to be that the form-elements of the blood are for the most part derived from the periblast, the primary corpuscles alone being moulded apparently from the detached cells of the subnotochordal trunks. In those forms in which a vitelline circulation is developed, the removal of nucleated periblastic cells and the formation of sinuous lacunæ (primary hæmal trunks) has been repeatedly observed, and may almost be taken as established. In those without such a yolk-circulation (and to them reference is in these pages chiefly made), the periblast also is seen in sections to break up into similar particles, and these doubtless pass into the sinus venosus, though in what way is not decided. Certainly the liver and alimentary canal, as well as the pericardial chamber itself, are, as already pointed out, in intimate relation to the periblast beneath the embryonic-trunk (Pl. VII. figs. 1, 2, 6, 9; also Pl. XII. fig. 8), and the transmission of detached periblastic elements into the circulatory plasma may be accomplished without difficulty. Ryder, in *Salmo* and *Tylosurus*, found such corpuscles in the pericardial chamber (No. 141, p. 537). This further consideration favours the latter derivation rather than the subnotochordal origin, viz., the rapid decrease in the volume of the yolk, even in those which have no yolk-circulation. In such forms the yolk protrudes as a very bulky appendage (*y*, Pl. XIV. fig. 1), but shortly before, and especially after the blood-circulation is visible, it diminishes very rapidly (*y*, Pl. XVII. fig. 1). Now, if before the hæmal fluid flows through its proper channels, it were deriving its corpuscles from the yolk, and still more, if with the further development of blood-vessels in the trunk a corresponding increase in the number of corpuscles takes place, the rapid disappearance of the yolk is readily accounted for. It is noteworthy, too, that while the subnotochordal trunks are the first to be developed, the formation of the subintestinal vein and cœliac artery quickly follows, and as these probably communicate with hepatic lacunæ, the periblastic elements would find easy entrance into the vascular system of the embryo. These nucleated cells, which make their way into the hæmal plasma, are originally colourless, and Lereboullet describes them as at first spherical, afterwards becoming flattened and elongated. They rapidly acquire the characteristic tint. In weak and sickly embryos the circulation is languid and the corpuscles few, a feature Lereboullet also noted (No. 93, pp. 581–2). In monsters, especially double embryos, the circulation presents interesting features, each having its own circulation, though receiving nourishment from a common yolk. Lereboullet instances the case of a trout (double monster) in which the artery divides into two vitelline trunks, each of the two returning as veins to the corresponding embryo; while in another case of a double-headed embryo, which possessed two hearts, one alone received blood from the vitelline veins, the other heart received nothing (No. 94, p. 246).

Renal Organs.—The differentiation of a renal tract takes place at a very early stage. We have seen that on each side of the notochord (Pl. IV. fig. 10) cuboid masses of mesoblast are serially marked off as protovertebræ (*my*) soon after the separation of the somatopleuric from the splanchnopleuric lamella. Just external to the protovertebræ, a little distance behind the otocysts, a rod of cells is budded off from the splanchnopleure

in close proximity to the intermediate cell-mass. Lereboullet observed that in *Perca* this structure develops earliest posteriorly, for he failed to trace it anteriorly, though at a later stage, about the time of hatching, he was able to follow its whole course (No. 93, p. 633) anteriorly and posteriorly. In some species a fold is developed, not a solid rod. Rosenberg seems to have been the first to speak of it as a diverticulum from the somatopleure (No. 138), and Oellacher, Hoffman, and others have confirmed this view. Ryder asserts that "the development of the renal organs in different genera of Teleosteans differs greatly in detail" (No. 141, p. 533), and this would certainly appear to be so, for in Salmonoids, which the observers named chiefly investigated, the origin of these ducts as longitudinal diverticula pushed dorsally towards the epiblast, as a groove-like fold, in fact, of the peritoneal cells, has been clearly shown (see Oellacher, No. 114, fig. 18_2, Taf. iv.; Hoffman, No. 69*a*, Taf. iii. fig. 3). Yet in Gadoids and Pleuronectids it is by no means clear that this is the precise mode of origin. In the earliest condition yet observed in these pelagic forms a longitudinal blastema or solid cylinder is formed on the outer margin of the intermediate cell-mass, just as we find in the chick. Defined at first in the region of the mid-trunk, this blastema rapidly extends forward to the pectoral region, but posteriorly it develops more slowly and is ill defined. A lumen is formed by the radiate arrangement of its cells, which separate at their common point of junction, and it is now outlined throughout its whole length some days before the embryo emerges. In an ovum (haddock) of the ninth day these structures are very distinctly seen as a pair of simple ducts, with walls consisting of a single layer of columnar cells, and extending from the pectoral region to the root of the tail. Anteriorly each tube is folded upon itself, turns inward towards the notochord, and ends in a trumpet-shaped infundibular opening, a condition exactly according with that described by Balfour and Parker in *Lepidosteus* (No. 18, p. 415); but in that species the authors agree with Rosenberg and Oellacher, that it is a hollow outgrowth of the somatopleure, and freely communicates with the body-cavity. The two ducts are widely separated, but as they pass backward gradually approach, and, curving down in the anal region, they meet and unite beneath the notochord in an unpaired common portion (*uv*, Pl. VII. fig. 8, and in section fig. 6*a*), which is originally of small capacity and provided with thick walls. At first the ducts are somewhat superficial (*prn*, Pl. VII. figs. 1, 2, 3), as is implied in their mode of origin, being dorsally directed outgrowths of the proximal somatopleure; but they undergo a change of position similar to that exemplified in the chick, and lie ventro-laterally to the notochord (*sg*, Pl. VII. fig. 4), and ultimately protrude into the peritoneal cavity (*sg*, Pl. XI. fig. 14). Ryder did not make out the mode of termination in *Gadus*, and he supposed that the urinary vesicle opens either directly into a cloaca or the terminal portion of the intestine. The continuity of the walls of the ducts (*sg*) with the bilobed upper part of the urinary vesicle (*uv*) is clearly demonstrated in section (Pl. VII. figs. 7, 11), and the urinary vesicle itself has an outlet in its early condition of an interesting nature. Lereboullet described in *Perca* the first condition of the ducts, and says that each must be a secreting

organ solely, assuming the excretory function later, when the ovoid dilation (urinary vesicle) establishes a communication with the lumen of the enteron (No. 93, p. 633). Kupffer draws attention to a strand of cylindrical cells connecting this receptacle and the hind gut, "uniting," he says, "with the epithelium of the gut" (No. 87, p. 224); but he appears not to have made out, any more than Lereboullet, an actual communication between the two. Yet such is the case. A distinct tubular connection exists; but the walls of the vesicle (*uv*) as well as the enteron (*hg*) are extremely plastic and mobile, vermiform movements being frequent, so that the lumen between the two becomes wider or narrower, and at times appears to close up, though the communication is usually readily seen (Pl. XX. fig. 13). Throughout their whole length, these excretory canals, including the urinary vesicle, exhibit simply a wall of nucleated cubical cells—a single layer of cylindrical epithelium. Such is the condition of the renal tract until the time of hatching, viz., a pair of cylindrical tubes, which pass along each side of the subnotochordal hæmal trunks, to terminate, after curving inward and downward in an infundibular opening. In front of the crozier-shaped loop (*prn*, Pl. XI. fig. 11, and Pl. XXI. fig. 6) a mass of trabecular tissue lies, into which tubules appear to enter to some extent, but this loose connective is also penetrated from the front by the growing basilar plate. The simple character of the embryonic renal organs in the Teleostei may be taken as evidence of a primitive condition, in which no metamerism is seen, the simple duct, which is truly an archinephric duct, forming a loop in front, and communicating with the pleuroperitoneal cavity, while posteriorly it passes into the hind part—a cloacal section, in fact—of the enteric tract.

During the greater part of embryonic life this simple condition continues, and the infundibular openings do not seem to increase in number; whereas in Amphibians several (three or four) are developed, and in Selachians they form a series. When the young fish emerges, the anterior end of the kidney shows signs of growing complexity, the folds of the loop increasing, and a vascular glomerulus being developed in front of the swim-bladder near each nephrostome. A little later the nephrostome of each side and its adjacent glomerulus are gradually enclosed in a capsule, this fibrous sac shutting off both structures from the general body-cavity. A section just behind the occipital region (Pl. XXVI. fig. 4) shows one of a pair of such capsules in the middle line and below the median hæmal trunks (*ao* and *cv*). On the lower and inner side of each capsule a vascular meshwork (*gl*) is present, while the nephrostome of the head-kidney opens on the outer side of the capsule. The rudiments of the single pair of glomeruli are seen in the newly emerged embryo, and are not fully developed until some days later; but in *Gastrosteus* and like forms, which issue from the ovum in a more advanced condition, the later features are already exhibited. Ryder states that in *Clupea alosa* there is no evidence of the existence of a nephrostome or of the presence of median glomeruli until long after hatching (No. 141, p. 534), and this is certainly remarkable, though in the Gadoids and others great variations are observable, the renal organs being fairly advanced in *P. platessa* a day or two before hatching, whereas in *P. flesus* and *P. limanda* they

are more rudimentary. The waste-products taken along the renal ducts originally pass directly from the body-cavity, but they are by and by conveyed from the special excretory Malpighian capsules into the urinary vesicle behind, a condition which remains essentially unaltered in the adult. The archinephric duct does not really close early in embryonic life, as has been stated (No. 48, p. 13), but opens into a special closed part of the body-cavity. With the further development of the anal region, the unpaired enlarged portion into which the ducts pass posteriorly communicates not with the rectum some distance from the external orifice as in the figure before referred to, viz., Pl. XX. fig. 13, but by a special passage with separate opening posterior to the anus, as in a cod the third week after emerging—a condition also shown in the gurnard three weeks old (Pl. VII. fig. 9). Of the series of segmental tubules and glomeruli seen in Elasmobranchs there is no trace in Teleosteans; but though the renal organs are so simple in these latter forms, the interpretation of the various parts is not devoid of uncertainty.

Teleosteans, it is generally held, agree with Cyclostomes, Amphibians, and Ganoids in possessing a pronephros; but, in all, it is a larval structure, and is supposed to disappear in the adult. We have seen that in the embryos of the Gadoids, flat fishes, and gurnards an anterior trabecular meshwork (*x*) lies in front of the archinephric duct, and that this duct itself exhibits a much convoluted fore end (*prn*, Pl. XI. fig. 11), with a nephrostome communicating with a glomerulus. The mid-portion of the duct becomes more or less convoluted, while the posterior portion remains comparatively straight, though on its dorsal side a large development of cellular tissue and small sinuous tubules takes place at a late or post-larval stage (Pl. XXIII. fig. 2).

In the adult we usually find an enlarged anterior paired structure, the head-kidney or pronephros succeeded by a pair of elongated bodies, indisputably renal, which are much swollen terminally, often united, and traversed on their ventro-lateral margins by a pair of excretory ducts. Balfour examined various species of Teleosteans in the adult condition, and came to the conclusion, in opposition to Rosenberg, that the so-called head-kidney is not truly renal, though he did not deny the persistence of the larval pronephros in the adult stage (No. 13, p. 15). In *Osmerus eperlanus*, *Esox lucius*, and *Anguilla*, the fore part of the renal mass consisted in the main of vascular lymphatic tissue, while the true kidney-substance extended posteriorly. In *Lophius piscatorius*, which, according to Hyrtl, possesses a head-kidney only, lymphatic tissue, traversed by tubules alone, was found. This lymphatic tissue may represent the convoluted enlargement of the archinephric duct, or merely a compact agglomeration of the loose cellular tissue lying external to the ductus Cuvieri and cardinal veins. It would appear that the latter is, in a large degree, true, the fore part being more emphatically trabecular, while the hind part consists of degenerate kidney-substance, so that Balfour's view most probably represents the facts, viz., that the so-called head-kidney is really a large lymphatic gland, concerned in the production of blood or lymph-corpuscles, while the hind portion is a remnant of the embryonic head-kidney. Except for certain lymph-spaces in the caudal region, the lymphatic system is but feebly represented in fishes, and

it is interesting to see a large glandular structure, such as the so-called head-kidney, which may be made out in early embryos, and which is from the first closely associated with the main hæmal vessels of the trunk. The lymphatic system, with its plasma and leucocytes, is really intermediate between a venous and an arterial system, and is associated with the various serous membranes, pleural, peritoneal, pericardial, and others. It is not surprising that large lymphatic masses should occur so near the centre of the blood-system, and though BALFOUR was not inclined to regard them as parts of the true kidney at all, they cannot at any rate be regarded solely as degenerate pronephric structures. WELDON, in his brief but interesting paper on *Bdellostoma* (No. 156), suggests that such masses are represented in all vertebrates by the suprarenal bodies. In *Bdellostoma* the archinephric or segmental duct is separated from this anterior mass, though in some specimens, possibly younger, traces of the continuity of the two could be made out. In embryonic Teleosteans the continuity is very patent, and in the adult condition renal tubules still ramify amongst the lymphatic tissue, as BALFOUR found in *Esox*, *Lophius*, and *Osmerus*. In the last species a single tubule alone passes into the vascular lymphatic mass. It would appear, indeed, as if the embryonic pronephros in the process of degeneration were usurped by the antenephric lymphatic structures, the proximity of both favouring this, while the persistence of stray tubules in the posterior part indicates the pronephric portion. GROSGLIK'S researches upon various adult Teleosteans (*Cyprinus carpio, Esox lucius, Rhodeus amarus, Gastrosteus aculeatus*) confirm BALFOUR'S view, as he found coexisting in the region of the head-kidney lymphatic tissue and remains of the atrophied pronephros surrounded to some extent by the cardinal vein, while some pronephric tubules still pierced the lymphatic meshwork (No. 60, pp. 605–611). EMERY, however, maintains that the pronephros persists permanently in such as *Fierasfer* and *Zoarces*; while in other forms, as *Blennius*, it is provided with glomeruli and tubules, and in *Merlucius esculentus* it presents the peculiar structure of the Wolffian body. In all it persists as a recognisable pronephros (No. 53*a*), a view which HYRTL held; while RATHKE and STANNIUS concluded that in *Cyprinus* the head-kidney is degenerate, and bereft of tubules, a view now generally adopted. The segmental duct precedes the development of the Wolffian body, and cannot therefore be a mesonephric duct, as BALFOUR suggests (No. 11, p. 701); it is in fact a pronephric duct, or more truly it is archinephric, for the pronephros is secondarily developed as a convoluted anterior portion. It is possible that this duct may not represent the primitive condition, but rather a segmental canal bereft of its serial segmental tubules and nephrostomes, save the single infundibulum at its anterior termination.* The view generally accepted however, is that which interprets it as a primitive non-metameric renal duct. The ducts retain their simple tubular character in the adult condition, and pass along the latero-ventral margins of the fully-developed renal masses. In the last larval stages, within a

* The fact, however, that some segmental tubes, consisting of nephrostome, capsule, and convolutions, develop in Elasmobranchs independently of the duct, and later connect by their originally blind end, may indicate that the serial condition is secondary. It illustrates at any rate their separation and independent coexistence, whatever the explanation may be.

month after hatching, mesoblastic cells become aggregated along the whole dorsal extent of the two ducts, especially in the fore and hind regions, and they present a somewhat glandular character, minute sinuous tubules appearing in their midst, which pass down and open into the longitudinal ducts. Plate XXVI. fig. 3, shows this elongated renal mass of segmental tubules, and presents largely the features of the permanent renal bodies. Still better is the relation of the parts seen in the section (Pl. XXV. fig. 3). The simple epithelial walls of the excretory ducts (*sg*) are fibrous and thickened, and become in fact the permanent ureters. Gegenbaur views the pronephros as the primitive excretory gland of the Chordata, whose place has been taken by the mesonephros, and we see that while the pronephric ducts persist the phylogenetic replacement of the pronephros by the Wolffian body is ontogenetically repeated. It is noteworthy that the segmental ducts become much convoluted along their course, but especially in the fore-portion. Whatever this may signify, these primitive archinephric ducts are the same as those which in Elasmobranchs and others connect the serial segmental tubes, but in Teleosteans they do not appear to divide longitudinally into upper or Wolffian ducts and ventral generative canals. The connective tissue which surrounds the renal organs becomes deeply pigmented at a very early stage (Pl. VII. figs. 1, 3, 4, and 7), the large black corpuscles continuing to increase until their structure in later embryonic stages becomes obscured on account of the profuse distribution of these bodies (*vide* Pl. XVII. figs. 1 and 2, and Pl. XXVI. figs. 3 and 4). The close connection of the early segmental ducts and the rudiments of the pectoral fin has been pointed out, and it is interesting to note that the black pigment, surrounding the renal organs at a later period, extends over and is continuous with the pigment-layer which passes to the base of the developed fin. The wall of the urinary bladder at a subsequent stage presents a consistent connective-tissue layer (*conn*), lined with columnar epithelium (*epith*), which in the upper portion forms prominent folds (Pl. XXV. fig. 5). These folds are continuous with the two excretory ducts, which, as formerly stated, open into the upper and anterior wall of the vesicle.

The Integument and Embryonic Pigment.—Throughout embryonic life the integument remains thin and transparent, so that the internal structure of the young fish is readily seen. No cilia can be detected upon it. As already pointed out, a flattened external layer or stratum corneum (*ep*, Pl. IV. figs. 5*a*–5*d*) is distinguished from the subjacent layer, the neurodermis (*ne*). Soon after the notochord is defined these two layers extend as a distinct integument, not only over the dorsum and flattened parietes of the embryo, but as a yolk-sac, over the vitelline globe (Pl. VII. fig. 6). The neurodermis, later in embryonic life, consists of several layers of pulpy rounded cells, which gradually merge into the flattened epidermis above. The innermost part of the two-layered epidermis constitutes a stratum Malpighii, and from it apparently exudes a lymphatic plasma, which forms a distinct fluid layer (*ss*, Pl. VII. figs. 1, 3, 4, 6), such a cutaneous sub-layer being found in *Amphioxus* and the Cyclostomes, though separated from the epidermal layers by the dermis proper. In Teleosteans when the mesoblast extends beneath the epidermis, to form the cutis proper, such a separation will be also

effected. There is, at an early stage, no true dermis beneath the Malpighian layer. Pouchet speaks of this subepidermal tissue as a soft variety of laminated tissue, having a very loose texture, and therefore little firmness (No. 119, p. 291), but in its earliest condition it is simply a soft semifluid stratum in which amorphous matter abundantly occurs. In this layer pigment develops (*pt*, Pl. IV. figs. 13, 20), and always appears as definite amorphous corpuscles, not a mere diffused solution.

In different species the early coloration shows very distinctive features, the colour of the pigment and its distribution being, in fact, so striking as to afford aid in diagnosis.

In some species the pigment is confined to the embryonic trunk (Pl. V. fig. 2); in others it extends over the extra-embryonic layer, *i.e.*, the yolk-sac (Pl. XVI. figs. 2, 8). Certain forms, again, exhibit one kind of pigment (Pl. XVII. fig. 1; Pl. XIX. fig. 8); others show two or more colours in the larval stages (Pl. XVI. figs. 1, 3, 5–9). No generalisation can be made, for in the same genus closely allied species show great diversity in these respects. Usually the pigment occurs in the form of minute isolated spots scattered upon the dorsum, and visible within one or two days after the closure of the blastopore; though it frequently forms superficial protuberances, evidently pushing out the epidermal stratum at certain points. The form of the corpuscles undergoes rapid changes; thus in a larval cod under examination two spots at the anterior border of the liver were seen to be finely branched, but before a sketch could be completed they visibly altered, and presented a simple rounded aspect.

In the cod (Pl. XIX. fig. 8) and haddock (Pl. XVII. fig. 1) black spots only occur. In the ova of the former species, seven days after fertilisation, these spots, amorphous or rounded in form, were scattered sparsely over the dorsum and lateral regions, but in a few days they multiplied and extended from the snout to the tip of the tail, without any regular disposition. In larvæ of the cod, soon after emerging, however, a further change in the distribution of the pigment takes place, for the spots, which are now elaborately stellate, become aggregated in four distinct bands (Pl. XIX. fig. 8), two very dense broad bands—a pectoral and an abdominal—occurring on the trunk proper; while the tail exhibits two less dense bands, and often indications of a third. The haddock never shows this regular series of dark bands, which seem to be so characteristic in the newly emerged cod. In the ova of the haddock on the eighth day (two days after closure of the blastopore), black spots are irregularly dotted over the dorso-lateral regions, and subsequent changes chiefly affect the number and form of the spots. A larva two days after emerging shows stellate spots of the most elaborate form, which send out complex ramifying processes. These spots appear on the cranial region, and very thickly in the post-otocystic and lateral regions of the trunk proper. Posteriorly they are chiefly confined to the lower half of the caudal trunk, only two or three large spots occurring above the level of the notochord. Occasionally one or two spots are seen to send processes into the fin-membrane. The whiting offers a great contrast to the foregoing Gadoids, since on the eighth day (three days after the closure of the blastopore) very faint yellow spots appear, and are thickly distributed over the entire trunk, including

the tail. Not only so; but the fin-membranes and the yolk-sac exhibit similar spots in abundance (Pl. XVI. fig. 2). They are very pale, and unless carefully looked for, readily escape detection, but they are very characteristic of this fish, even in the late larval stages, the pale yellow, with a distinctive greenish tinge rendering them important for diagnostic purposes. In this species one or more enucleate, elaborately stellate structures frequently exist on each side of the mid-mesenteric region. Sometimes five or six of these bodies appear upon the surface of the yolk near the trunk of the embryo. They have the form of a "bone-corpuscle," but they are not pigmented, and their nature and meaning are doubtful. In the ling, from the third to the fifth day (Pl. XIX. fig. 9), while the blastopore is closing, neutral-tinted amorphous spots, apparently protoplasmic aggregations, which send out pseudopodial processes, and thus acquire a rudely stellate form, occur over the yolk-surface (*vide* Pl. XIX. fig. 9). Two days later (when about thirty protovertebræ are segmented off) the trunk and fin-membranes are very richly supplied with yellow pigment of a bright canary-tint (Pl. V. fig. 9). This consists of unbranched corpuscles, and extends also over the yolk-membrane. Black pigment likewise appears, a few rude spots at first behind the eyes, and similarly it is not confined to the trunk, stray stellate spots extending over the yolk-surface, and especially over the protoplasmic covering of the large oily sphere (*og*). On the trunk, from the otocysts (*au*) to the tip of the tail, a more or less regular linear series of stellate black spots passes, extending at times over the dorsum. In *Motella*, as Mr Brook (No. 31, pl. ix. figs. 7, 8*a*; pl. x. figs. 10, 11) has shown, black pigment occurs in definite patches; and after the embryo has emerged, this definite aggregation of the spots produces a very remarkable appearance (Pl. XVII. fig. 2).

In the few species of Pleuronectidæ as yet investigated, certain common features are noticeable, viz., the general occurrence of yellowish pigment (*vide* Pl. V. fig. 6; Pl. XVI. figs. 1, 3, 5, 6; Pl. XVIII. figs. 1, 2; Pl. XIX. fig. 5), and in later stages the presence of two distinct colours (Pl. V. fig. 6; Pl. XVI. figs. 1, 3, 5; Pl. XVIII. figs. 1, 2). On the fifth day (120th hour after fertilisation), when twenty-two to twenty-five protovertebræ in the common flounder are marked off, pigment of a pale brown tint, yellow by transmitted light, occurs on the sides, especially along the median lateral line. Twenty hours later, black spots, very minute in size, appear, intermingled with scattered yellow spots over the trunk and tail. The yolk, however, is devoid of pigment. Pl. XIX. fig. 5, shows the arrangement of the yellow pigment at the time of hatching. In examples at an advanced stage, *e.g.*, twelve or fourteen days after hatching, a remarkable distribution of these spots is exhibited (Pl. XVI. fig. 1). The brownish yellow spots extend above the mid-brain (*mb*), around the eyes, along the mandibles, and over the abdominal region; but are especially aggregated along the dorsum upon each side of the median fin. The peculiar patches of radiate or stellate yellow spots which appear midway along the embryonic caudal fin-membranes, dorsally and ventrally, will be described in a subsequent page (*see* Median Fins). Radiate black spots also occur amongst the yellow pigment.

The dab (*Pleuronectes limanda*) has a distribution of pigment similar to that in the flounder, though the yellow spots seem to take a more distinctive linear disposition, two lines running along each side of the embryo, the upper line marking the dorso-lateral limits of the neurochord (Pl. V. fig. 11). This distribution is well seen when the embryo is viewed from above. Pigment (yellow) appears when about thirty protovertebræ are outlined (*i.e.*, about the seventh day after fertilisation). On the fourteenth day (two days after emerging) the pigment-spots around the margin of the eyes and the otocysts coalesce to form larger patches, irregular in form. A few days later, the upper lobe of the caudal membrane is diversified by the development of an undulating line of yellow pigment, or rather of a linear series of crescentic patches. Other spots occur thickly in the anal region, but the yellow pigment of the trunk is confined for the most part to two lines, as above described (Pl. XVI. fig. 6). In a more advanced embryo, thirteen days after extrusion, the crescentic series of patches in the caudal fin is still more boldly marked, while two or three irregular touches appear on its lower lobe. The stellate pigment-spots are now meagre, occurring, as in the earlier stage just described, over the eyes, along the ventral region, over the greatly diminished yolk-sac, and very sparsely on the tail. The eyes have become darker, by increase of their black choroidal pigment, and about this time they show a striking green lustre in oblique light (Pl. XVI. fig. 3).

In the plaice (Pl. V. fig. 6) black pigment-spots, mingled with finely stellate bright canary-yellow corpuscles, develop, though comparatively late, and when the embryo is freed it does not show the marked pigmentation of the cod or like forms. On the third or fourth day after emerging yellow pigment appears as very minute amorphous spots. In Pl. XVI. fig. 5, the peculiar distribution of the two tints is seen. The head and trunk present very minute, scattered spots. The ventral margin of the alimentary tract shows stellate black spots; while the upper and lower contours of the caudal region have bold lines of stellate spots, which extend to the caudal fin-membrane, though confined to the lower lobe, and here the spots are simple and very minute. The yellow pigment appears only as a narrow area towards the end of the tail, viz., the upper margin of the posterior half of the caudal trunk. At the root of the tail a dense patch of black spots occurs, extending obliquely just above the urinary vesicle.

Pigment appears in the gurnard at a slightly later stage than in the foregoing forms. It consists of very pale yellow spots, which have a delicate sea-green tinge in certain lights. They are sparsely scattered over the trunk proper, but form a rude line along the dorsum, and an undulating line along the sides and around the eyes. Three or four days later minute black spots occur, and both colours are sparsely distributed over the yolk-sac, and around the large oil-globule. A more advanced embryo is seen in Pl. XVI. fig. 8, at which stage irregular patches of yellow and black pigment exist upon the dorsal and ventral portions of the caudal membrane. The spots send out branched ramifying processes, and the pectoral fin exhibits distally a radial yellow and black coloration. The eyes, however, are very slightly tinted with minute black spots. In still later larval and post-larval stages the pigment diminishes, and only occurs very

sparsely in linear areas along the summit of the head, the opercular region, and on the snout. In form the spots are amorphous or rudely stellate. Along the huge pectoral fins and the ventrals similar minute corpuscles are developed, mingled in the former pair of fins with yellow pigment-spots (Pl. XVII. fig. 5).

Certain features in the development of the pigment are noticeable, such as the fact that in some Gadoids the spots are confined solely to the trunk (cod, haddock, and rockling), (*vide* Pl. XVII. figs. 1, 2); while in the whiting (Pl. XVI. fig. 2), the sole and the ling (Pl. V. fig. 9), the covering of the yolk (*y*) becomes richly pigmented. This pigmentation of the yolk-sac is a feature also in the gurnard (Pl. XVI. fig. 8), and in the latter and the ling coloration is preceded by the appearance of colourless corpuscles, which are scattered over the yolk-sac (*vide* Pl. XIX. fig. 9). Pale neutral tinted bodies, evidently protoplasmic, and of various angular shapes, are distributed over the yolk-surface. They send out pseudopodia, and become rudely stellate. In the ling this occurs on the fifth day after fertilisation—about the time that the blastopore closes; and in the gurnard at a similar stage these protoplasmic particles with short processes also appear. These bodies are obviously only a cortical disposition of protoplasm—less delicate and complex than the elaborate network of protoplasmic threads which extends over the yolk-sac in the cod, haddock, flounder (Pl. XIX. fig. 5), dab (Pl. V. fig. 3), and other forms.

The pigment-spots which occur over the yolk-surface are beneath the cellular germ-layer. They develop, as Ryder has pointed out, in the non-cellular periblast; and Cunningham, while noting this condition, viz., that "they are situated at the surface of the periblast," in *Pleuronectes microcephalus* and *Scomber*, states that in the latter species the pigment is confined to the deep surface of the oil-globule and the sides of the embryo.

If the large multipolar corpuscles in the ling and gurnard be merely the nodes or thickened points of intersection for the protoplasmic threads crossing over the whole yolk-surface, it is remarkable that these points of intersection should not develop pigment in the cod and dab, whereas they apparently become the pigment-spots of the yolk-sac in the ling and gurnard. The actual transformation of the colourless corpuscles into pigment-spots was not observed, but it is very probable.*

The pigment-spots of the embryonic trunk often form distinct papilliform projections, the growth of the corpuscle pushing the epiblast out, and forming a small mound at that point. If the development of a pigment-spot be followed in the ling or gurnard (*vide* Pl. V. fig. 2), we see a rounded or irregular particle of clear protoplasm superficially placed upon the yolk-surface, which shows amœboid movements, and sends out blunt processes (Pl. I. figs. 8*a*, 8*b*). These processes become bifurcate, and assume a more or less elaborate ramose disposition—a stellate corpuscle being the result (Pl. V. fig. 2*b*). In the

* In *Gastrosteus* Kupffer speaks of the appearance on the yolk-surface of small nuclear bodies, from which he says not only pigment, but blood-corpuscles are formed. These nuclei, probably the nuclear bodies already referred to in the allied marine species (p. 55), which become radiate in form, develop pigment-particles, the others keep their original shape until they are set in motion by the establishment of a blood-circulation (No. 88, 1868). In *Gastrosteus spinachia*, the yolk-cortex, even before the blastopore closes, presents a striking appearance on account of the large translucent nuclei which are scattered all over it. These nuclei often show many nucleoli (*vide* No. 124, p. 493), and in the freshwater species, *G. aculeatus*, a reticulation is also present, but this has not been observed in *G. spinachia*.

centre a nuclear portion (*n*) can be made out, and this usually remains clear and unchanged, while around it very minute particles of black pigment (*pt*) develop. These particles increase so rapidly that the bases of the pseudopodia become much darkened, and a centrifugal transference commences, the minute particles flowing along the ramifying arms, until a pale steel-tinted stelliform body becomes distinctly outlined. The tint grows in intensity, and finally shows the dense black colour characteristic of the completely developed corpuscle. In many cases by their extension these black corpuscles intermingle so as to interlace their arms in a complex manner, and even coalesce, as was noticed by Lereboullet, who also observed the persistence of the central pale nucleus in each corpuscle (No. 93, p. 579).

The variations in the disposition of the pigment in different forms is noteworthy, and its diagnostic utility has been already mentioned. The time at which pigment appears is also remarkable. Lereboullet found in *Perca* that it develops earlier and more abundantly than in *Esox*, though in both forms it overspreads the yolk-sac (No. 93, pp. 579–586, 610). It is very precociously developed in the flounder, and comparatively late in the whiting.

During the later larval stages the epidermis becomes very irregular—rounded protuberances appearing especially over the cranial and facial regions (Pl. IX. fig. 3; Pl. XVII. fig. 4). Many of these are sensory enlargements, and described elsewhere, but enlarged mucous cells develop, especially in the region of the snout. These open superficially, and doubtless are protective in function—bathing the young embryo externally with a gelatinous secretion. The contents of these large mucous cells stain very deeply, and are especially noticeable in sections of the plaice, though in *Cyclopterus* and others they also form a noteworthy feature.

No cilia are apparently developed upon the embryonic integument, nor do fine immovable hairs occur as in *Petromyzon* and its young stage—*Ammocœtes*. The serial sensory papillæ (Pl. VI. figs. 8, 8*a*) send out fine filiform processes (*plp*), but they are local, and probably pushed through from the neurodermis below. The development of scales as protrusions from the corium which burst through the epiblastic integument, as well as the formation of iridescent plates in the stratum Malpighii, belong to a late post-larval stage. In some young forms, it is true, a brilliant iridescent appearance is seen in the abdominal region; but this is occasionally due to the enlarged swim-bladder, the fishes in certain cases remaining translucent, and almost colourless in the post-larval stages, when all the more important structural features of the adult are assumed. In such forms, again, as the post-larval *Anarrhichas*, the whole abdomen is iridescent.

Ova and Generative Organs.—As soon as the segmental ducts have reached their final position on each side of the dorsal aorta, a strand of peritoneal (splanchnopleuric) cells passes below them. They thus become grouped on the inner side close to the mesentery (Pl. VII. fig. 1). These cells become aggregated, and produce an irregular contour especially in the posterior region—where the alimentary canal is more distant from the notochord, and the median mesenteric membrane is better developed. They

form, in fact, the germinal epithelium, but a definite germinal ridge cannot be made out. Indeed, in the haddock, it is not until the second or third week after extrusion that this germinal portion becomes distinctively marked (Pl. XI. fig. 14). Some of these cells (*po*) are seen to enlarge and protrude from the surface of the mesentery (*msn*) into the abdominal cavity as large primitive ova, and they occur, almost solely, slightly anterior to the urinary vesicle, especially above the region of the small intestine. In short, their appearance and distribution precisely accords with BALFOUR's description of the early Elasmobranch ovum (No. 15, vol. xi. p. 161). The ova are most closely grouped on the roof of the abdominal cavity, and especially in the median niches formed by the projection of the suspensory septum or mesentery (*msn*). They are also grouped upon the mesentery, and some develop upon or have migrated to the peritoneal envelope of the intestine itself (*hg*). They are very irregularly distributed, and show great variation in size; large spherical ova projecting from a mass of small undeveloped cells, and all loosely held together by the delicate connective tissue of the peritoneum. The ova appear to be like the cells adjacent, and differ only in their larger size and more active development. Each consists of a mass of minute nucleated spheres enclosed in a thin membrane; but are quite unlike the primitive ova of Elasmobranchs, as described by BALFOUR (No. 13, p. 164), for these latter are uninucleate, one or two nucleoli, staining deeply, occurring in the nucleus, which is large, and surrounded by a granular protoplasmic matrix. Along each side of this region of the abdomen, external to the abdominal cavity, a mass of cells may occur, not unlike, but less in dimensions than, the primitive ova described above. The lateral niche in which they are aggregated is defined by richly pigmented peritoneum, and this pair of lateral sacs strongly suggests the ovaries of the adult. The largest ova are those, however, which are free, and project boldly from the mesentery and roof of the abdomen. BALFOUR speaks of a thickened germinal epithelium in the Teleosteans, into which the adjacent stroma sends ingrowths—the cells of the epithelial layer increasing by the growth of the clear protoplasmic contents. But this does not correspond with the condition seen in the young haddock, each ovum being a more or less perfect sphere, and enclosing numerous minute nucleated bodies. Later stages were not observed, and it was not made out whether the lateral peritoneal sacs finally became the ovaries with their continuous genital ducts, or whether an epithelial layer grew over the freely suspended primitive ova, and enclosed them in an ovarian sac, depending from the abdominal roof.

IX. The Fins.

Median Unpaired Fins.—The development of a median epidermal crest (*ef*, Pl. V. fig. 11; Pl. XIII. fig. 3; Pl. XIX. fig. 10), extending along the median dorsal line from the cephalic region round the end of the tail, and along a portion of the under surface of the caudal trunk, is an early and noticeable feature in the embryos of Teleostean fishes, with probably few exceptions (*e.g.*, *Hippocampus*). Soon after the tail is detached from the yolk-surface, within a day or two after the closure of the blastopore, a minute fold of epiblast projects as a ridge along the whole course just indicated. It grows in vertical breadth, being pushed out in the form of an epiblastic fold, and shortly before the extrusion of the embryo is quite a broad membrane, especially well developed in the hind trunk and caudal region. On account of its superficial extent—while the embryo is within the egg—it is creased and much folded about the body; but on the embryo issuing from the ovum the membrane rapidly straightens out and becomes erect. It apparently continues to grow after extrusion, a newly hatched embryo having a much less extensive median membrane than one a few days old (compare Pl. XIX. fig. 5; Pl. XIII. fig. 6; Pl. XVI. fig. 1). The extent covered by this fin (*ef*) varies in different species, thus in the young of *Trigla gurnardus* (Pl. XII. fig. 1) it never extends quite so far forward as in the forms, *e.g.*, *Gadus æglefinus* (Pl. XIV. fig. 1), *G. morrhua*, *G. merlangus* (Pl. XVI. fig. 2), and *Motella* (Pl. XVII. fig. 2); its wider portion in fact reaching only to the otocystic region, in front of which its height gradually diminishes, and the fin disappears above the occipital region (Pl. XVI. fig. 8). In such examples as the Gadoids just mentioned, it is broad and prominent as far forward as the mid-brain, in which region it gradually slopes to a mere ridge. The thinness and transparency of this structure is remarkable. It is so delicate that as the fish progresses through the water it is flexed and waved about with every movement, and on removal from the water the fin collapses at once, and lies like a film on the body. Slight contact with a hard substance immediately injures it, and while in healthy larvæ it stands out erect and even, and is perfectly translucent, it appears crumpled and in many parts opaque when the fish is in a sickly or dying condition, ultimately dissipating or breaking up into needle-like fragments.

In certain forms, *e.g.*, *Gadus merlangus* (Pl. XVI. fig. 2), *Molva vulgaris* (Pl. XVII. fig. 9), and *Solea vulgaris* (Pl. XVII. fig. 13), the pigment, which extends not only over the body, but over the yolk-sac, appears also upon the embryonic fin (*ef*); whereas in *Gadus morrhua*, *G. æglefinus*, &c., no such pigment-corpuscles occur save on the trunk of the fish—the yolk-sac as well as the membrane being destitute of them. It was mentioned previously that in *Pleuronides limanda* (Pl. XVI. figs. 3, 6) and *Trigla gurnardus* (Pl. XVI. fig. 8) the fin shows during the later larval stages remarkable coloration—in the former species crescentic particles of yellow pigment appearing in regular series along the membrane above and below the caudal trunk during the second week after

hatching, while in the gurnard a third-day embryo shows irregular patches of yellow pigment, with which black spots are also mingled (Pl. XVI. fig. 8). The coloration in other species will be noticed on a following page.

In transverse section this fin-membrane (*ef*) consists merely of a simple median fold of the double-layered epiblast—the outer flattened corneous layer, and the inner sensory layer, which proceeds into the narrow fissure separating the two lamellæ of the fin (Pl. VII. figs. 3, 6). This fissure enlarges close to the trunk, and is continuous with a spacious subepidermal chamber which extends all round the latter, and is well seen in late larval stages in section (Pl. VII. fig. 6) and surface view (Pl. XVI. figs. 1, 3). A jelly-like lymph fills up this cavity, which, as already pointed out, becomes extraordinarily enlarged in the cephalic region. All along the trunk such a space exists in a modified degree, and delicate nerve-strands pass across it from the spinal cord to the sensory papillæ in the skin. Along the tail the interspace is narrowest (*ss*, Pl. XI. figs. 15, 17), but on the ventral side, as the root of the tail is approached, it enlarges and forms a spacious fissure in the anal region (*ss*, Pl. XI. fig. 14). It is in this chamber, limited on each side by the epiblastic fin-fold, that the rectum (*hg*) pushes its way, and before the anus is formed sends out a strand of loose cells, extending from the base of the urinary vesicle to a point midway down the expanse of the fin-membrane.

The hind gut, as already indicated, ends blindly, and does so for a period varying very much according to the species. The anal column of cells, before and after a lumen is formed, passes down the centre of the fissure (*ss*), and is apparently held in place by the tenacious plasma (*x*, Pl. VII. figs. 12, 13), in which granules subsequently appear, and forms a matrix surrounding this part of the intestinal tract. As formerly mentioned, the anus does not extend to the ventral margin of the fin, but opens at the side about midway (*a*, Pl. VII. figs. 14, 15). In this continuous embryonic fold the permanent unpaired fins of the adult fish are formed—arising, as Balfour said, by local hypertrophy (No. 11, p. 78), though no less by atrophy of the parts between the ultimate fins. Lereboullet refers to this atrophy in *Perca*, when he says the margin becomes indented where the three vertical fins in that species will finally remain (No. 93, p. 634). These local indentations mark the atrophy of parts of the embryonic membrane, which finally disappear, leaving the prominent and strengthened remnants of the once continuous fin to form the permanent unpaired fins. Before this atrophy of the transient portions and the hypertrophy of the permanents parts, the sites of the ultimate fins often appear to be indicated by remarkable aggregations of pigment. Thus, in the advanced embryo of *Pleuronectes flesus*, a striking development of pigment-corpuscles takes place in the dorsal and ventral portions of the embryonic fin. Scattered pigment occurs along its whole extent behind the pectoral region, though it is sparse; but certain parts in an early stage are distinguished by more abundant coloration, and in the thirteenth-day flounder, referred to, a patch of brownish-yellow pigment-spots, arranged in a radiate manner, is seen with black spots intermingled (Pl. XVI. fig. 1), as also in the undetermined Pleuronectid figured on Pl. XVIII. fig. 1, and in *Agonus* on the

same plate, fig. 11. A similar dorsal and ventral arrangement of caudal pigment-spots occurs in the advanced embryo of the ling (Pl. XVII. fig. 10), black pigment-spots diverging upward and downward from the caudal trunk in a characteristic manner. In this way the sites, so to speak, of the future median fins are indicated by radiate coloration before the continuity of the embryonic membrane (*ef*) is to any appreciable extent destroyed. Later, however, the developing fin-rays (embryonic) are more clearly indicated by granular striations which pass across the membrane (*vide* Pl. XIII. figs. 2, 6*a*; Pl. XV. figs. 4, 5), still very thin and transparent (though a fine reticulation of a superficial character often appears in it), no mesoblast having as yet insinuated itself into the interlamellar fissure, as shown in a section of the haddock on the third day after hatching (Pl. VII. figs. 3, 4), or even so late as the seventeenth day (Pl. XI. fig. 14). Lereboullet noticed similar indications in the still persisting membrane of the embryo of *Perca* when twelve to fifteen days old. He describes along its whole length small irregular transparent structures like oil-tracts, and he found that they accumulate where the permanent fins will be developed (No. 93, p. 640). These are either the homologues of the pigment-corpuscles mentioned above, or aggregations of the external reticulation. Later, he says, he noticed these disappear in *Leuciscus euryophthalmus* as if by absorption, and striations inclined in a backward direction take their place. They form successive pairs, the rudimentary rays, in fact, of the unpaired fins, which he remarks are double at the time of origin (p. 640). Ryder speaks of the mesoblast as entering the fold at an early stage (No. 114, p. 517),* but this does not apply to many forms, for a section through an advanced embryo of the haddock, as just mentioned (Pl. XI. fig. 14), still shows a mere epiblastic fold (*ep*) little altered from its primitive condition. While the membrane still remains thin and translucent, ray-like thickenings are frequent—apparently aggregations of a horny or chitinous nature, usually regarded as epiblastic thickenings, which develop, as Lereboullet observed, centripetally, and grow towards the trunk (No. 93, p. 637). He describes them as transparent strips, distant from, but directed towards the body, and appearing simultaneously in the three parts which subsequently form the three vertical fins in *Leuciscus euryophthalmus*. These rays Lereboullet describes as formed by a "condensation of a plastic material without any grouping of cells," and he regards them as connected with the vertebral column below from which they are separated, subsequently, by the interspinous bones (p. 630). In reality, however, the early rays are merely dermal thickenings, and appear at first as narrow granular tracts indefinite in outline, and extending dorsally and ventrally, and therefore unconnected with the axial skeleton below. Lereboullet's view applies to the dense permanent rays which develop in the post-larval stages, for these rods are paired, and arise under the epiblast—beneath the pigment, which appears in the Malpighian layer of the ectoderm, and are most probably aggregations of mesoblastic cells which grow up into the median fin-fold from the axial (skeletal) mesoblast below. In

* Ryder now holds that even the embryonic fin-rays are mesoblastic (*Rep. U.S. Comm. Fish and Fisheries*, 1884). As fast as they appear, they are preceded or accompanied by outgrowths of mesoblastic cells.

the embryos of species with pelagic ova, *e.g.*, *Gadus morrhua*, *G. æglefinus*, *G. merlangus*, *Molva vulgaris*, *Trigla gurnardus*, and the Pleuronectidæ, such median fin-rays do not appear even in the late larval condition (*ef*, Pl. X. figs. 1, 4; Pl. XVII. figs. 2, 10, 12); and Ryder instances other examples, some having demersal ova, *e.g.*, *Alosa*, *Pomolobus*, *Cybium*, *Parehippus*, and *Idus*, in which this is so (No. 141, p. 518), the original transparent membranous condition of the embryonic fin persisting to a late stage. Ryder adds that in *Gambusia* and certain Lophobranchs no embryonic fin-fold is formed at all—the single dorsal fin arising later as a local dermal excrescence with a core of intruding mesoblast (No. 141, p. 518). In some Cyprinoids (*Idus* and *Carassius*), which also possess a single dorsal only, the continuous embryonic membrane nevertheless appears. Pl. XVII. fig. 5, represents a young gurnard in which the two dorsals and the single anal fin (*af*) are indicated; but the former are still continuous with the tail-membrane (*cf*), while a remnant passes forward to the anal fin. The stage figured is post-larval, and in Pl. XVII. fig. 7, the fins have really reached the adult condition, and are completely differentiated, all trace of the continuous embryonic membrane having disappeared. In Pl. XV. fig. 6, representing *Cyclopterus lumpus*, these intermediate connections are still discernible, though the two dorsals (*df*) and the anal are almost wholly separated. These unpaired fins have become conspicuous by hypertrophy at three points, and by the atrophy of the membrane in front and behind (see also fig. 5). The ventral median fin is broken up into two by the anus (*a*), which, *e.g.* in *Gastrosteus*, has pushed its way down and terminates at the apex of an angular bay marking off a pre-anal from a true anal fin (Pl. XV. fig. 5). Lereboullet describes such a bay in the newly emerged embryo of *Perca*, while the body is still encircled by the continuous fin, "the lower edge," he says, "exhibits an indentation where the anus will appear" (No. 93, p. 616). This condition differs very much, it is unnecessary to point out, from that in the newly hatched embryos of the species here described. A post-larval flounder, 5·8 mm. in length, which is perfectly translucent and colourless, but has lost almost every embryonic trace, still retains a membranous vestige connecting the dorsal above and the anal below with the caudal fin. The three fins thus connected have otherwise attained all the characters seen in the adult.

The unpaired fins in Teleosteans, therefore, do not arise as two apposed, independent epiblastic plates, but as a median fold or crest.

Prof. Humphry first broached the idea, from an examination of the adult anal fin, that it might be double in its origin, *i.e.*, a union of two lateral fins; and he suggested that the other median fins might have thus originated, and that the paired and unpaired fins were alike double primitively (No. 72), a view supported by the fact that the dorsal fins, in addition to their (spinal) motor nerves, are supplied by a pair of sensory nerves which branch off from the trigeminal soon after it emerges from the roof of the skull. The study of their development, however, would seem to yield an opposite conclusion—the median fins are single at their origin,* and their bilateral structure—muscular and

* Lereboullet's statement that the dorsal fin is double at its origin is likewise misleading (No. 93, p. 630).

skeletal—is subsequently assumed, and it must be added the paired sensory (nerve) connection, above mentioned, is probably also secondary, for in Selachians and Dipnoans no trace of it is seen. It is remarkable that in some forms, *e.g.*, *Apeltes*, vascular loops are formed in the median fin-folds at the time of hatching, whereas in none of the species specially referred to in this paper is this the case—the membranes remaining transparent and non-vascular for some time after extrusion.

The Caudal Fin.—It is plain from the foregoing observations that the tail of the embryo is not by any means distinctly marked off from the trunk. The tail is indeed the tapered portion of the trunk, which gradually diminishes, ending posteriorly as a thin rod (the notochord with the muscle-plates on each side), and the neurochord above (*cf.* Pl. XIII. figs. 1, 2, 4, 6*a*, 7). A strand of connective tissue passes along beneath the rod, and in this tissue the hæmal trunks of the tail are by and by formed (*vs.*, Pl. VII. fig. 6*a*; Pl. XI. figs. 15, 17). The whole is encircled by the embryonic fin-membrane (*ef*) which passes along the median dorsal, terminal, and ventral line, so that the tail is at this early stage of the typical protocercal type, showing no division into lobes. In the early ling, about the time that the eyes are fairly complete, two peculiar folds are sent off below the muscle-plates in the caudal region. While within the ovum the caudal trunk lies for some time as a flattened process upon the yolk, its greatest breadth being at right angles to the caudal plane of symmetry, and when first it buds out from the trunk it is in a state of torsion, the developing fin-membrane being folded in a complicated manner at the root of the tail, and passing as a horizontal ridge round its termination (Pl. II. fig. 11). This state of torsion, which is very marked in the earliest condition of the tail, does not continue, and shortly before hatching the enlargement of the preivitelline space not only gives the caudal trunk more freedom, but even permits active movements on the part of the embryo.

Usually, as pointed out above, the trunk terminates in a more or less accuminate process (Pl. XIII. figs. 1, 2, 4, 6*a*, 7); but in Pl. XV. fig. 4, a remarkable terminal enlargement is seen, the neurochord swelling to form a lobe, while the notochord ends in an irregular bulbous structure. In the figure just referred to (Pl. XV. fig. 4) the tail-fin proper is marked by a radial structure (embryonic fin-rays), apparently a mere dermal thickening, such as we see in a late stage of *Pleuronectes limanda* (Pl. XVI. fig. 3). In Pl. XIII. figs. 6, 6*a*, the embryonic membrane is diminished between the terminal caudal and anterior portions, and a mass of granules is forming around the end of the notochord, which assume a radial disposition. These diverging granular tracts are better defined, and form, in fact, rays in the dorsal and ventral lobes of the membranous fin of the same embryo (Pl. XIII. fig. 7). The formation of fin-rays, without the intervention of special cellular prolongations from the vertebral arches, was observed by Lereboullet, who speaks of them as produced probably by "the deposit of a cartilaginous cytoblastema" (No. 93, p. 634). The appearance of these rays does not suggest a cartilaginous character, the fine granular tracts (Pl. XV. fig. 5), as they become defined, form clear translucent rods (Pl. XIX. figs. 2–4), not unlike the "spicular substance,"

which appears in certain parts of the axial and appendicular skeleton (*e.g.*, vertebral bodies and pectoral arch). Most probably they are of a resistent horny (?) nature, and they are developed at first in the distal or mid-part of the fin-membrane, approaching, as before pointed out, the trunk by the growth of the proximal end of each ray, "their development being in conformity with M. SERRES' law of centripetal formation" (No. 93, p. 634; also *vide* SERRES' *Principes d'organogénie*, Paris, 1842, p. 212). As the rays thus develop, the aboral end of the cellular notochord (*nc*) curves upward (Pl. XVIII. fig. 3), the upper lobe (opisthure of RYDER) diminishes, while a new and larger lobe expands on the ventral side of the chorda. A notch, however, separates this new growth from the lower lobe of the primary protocercal tail (Pl. XIX. fig. 4).* AGASSIZ describes this development of the secondary caudal membrane as an atrophy of the upper lobe, and a rapid development of the lower lobe which becomes bifid. The lower lobe does not really become bifid, but a new lower or rather anterior ventral lobe grows out, and by its rapid development leaves a notch separating it from the primary lower lobe. The two original lobes of the protocercal tail are gradually pushed further up and almost entirely disappear, the tail of the adult being for the most part a wholly new growth on the ventral side of the notochord, and slightly anterior to its termination (compare figs. 3 and 5, Pl. XVIII.). The stages of this atrophy of the primary fin-lobes and the growth of the secondary tail-fin, mainly as a new product, can be seen by comparing Pl. XVII. fig. 3, which shows the original protocercal outline, with fig. 6 on Pl. XV., in which the secondary tail-fin is formed as a large ventral lobe supplanting the primary tail. In fig. 5, Pl. XVII., the new tail-fin has completely taken the place of the primary membrane. Pl. XVIII., figs. 3, 4, 5, and 7, show these stages well. The embryonic tail with its dermal rays is transitory, and the permanent tail with its hypural elements (Pl. XV. fig. 3) belongs to a stage which is post-larval. LEREBOULLET says the materials out of which these later skeletal elements are developed are furnished by a rich caudal plexus of blood-vessels. This complex vascular development, he says, "precedes and announces the formation of the tail," and it consists of a system of elongated loops in the pike, perch, trout, and roach (No. 95, p. 26). No such subnotochordal terminal plexus is formed in the Gadoid and other forms studied at St Andrews. Thus the gurnard, even at so advanced a larval stage as Pl. XVII. fig. 5, shows no such network; yet the hypural plate is well developed and the fin rays fully defined.†

The Paired Fins.—When the embryo is first outlined in the blastoderm, an alar expansion stretches away on each side of the trunk of the young fish. This expansion consists of epiblast and hypoblast resting upon the stratum of periblast below. No

* RYDER ("Evolut. of Fins of Fishes," *Report of Com. Fish and Fisheries for* 1884–1886) states that there is evidence of the degeneration of the caudal region, as in *Chimæra* and *Stylephorus* there is a permanent archicercal opisthure, a large temporary one in *Lepidosteus;* and, moreover, there is the evidence of the concrescence of the hypural pieces; the ventrally diplacanthous and even triplacanthous caudal vertebra, or their coalesced representative, the urostyle; the existence of hypaxial opisthural elements; the abortion of the epaxial spines of the caudal vertebræ; and finally, the abortion or extreme modification of the last muscular somites of the caudal region. RYDER (*op. cit.*, from an examination of the eel) holds that the hypurals are partly hæmal and partly interspinous.

† See LOTZ on "Tail of Salmon," &c., *Zeitschr. f. wiss. Zool.*, 1864, p. 260.

mesoblast apparently extends into it (*al*, Pl. III. figs. 11–13; Pl. IV. figs. 4, 10), though this layer is ill-defined laterally at this stage. A pair of lateral horizontal alæ (*al*), indeed, stretch along the whole trunk—from the pectoral to the post-mesenteric region. It is in reality the elongated and narrowed blastodermic scutum (Pl. XXVIII. fig. 5), and extends in front and behind the two points mentioned, though it is there thinner and hardly distinguishable. In Pl. III. fig. 19, such a pair of lateral horizontal fin-expansions are present extending from the trunk-region proper, and their limits are very definite when viewed from above. Just as in the case of the median vertical fins, certain areas in these horizontal alæ become defined, as special fin-regions by a visible thickening, apparently from the folding under of the epiblast. Thus two flattened oval pads consisting of a double epiblastic fold like the double median fin-fold, are disengaged from the rest of the alar expanse. Before and behind this pair of pads the lateral membrane thins away and atrophies, while the special portions continue to increase in density as a pair of pectoral limbs (*pf*, Pl. V. figs. 6, 9; Pl. XIV. fig. 1). Lereboullet apparently did not notice that the pectoral fins emerge from the lengthy lateral membrane or alar expanse on each side, and speaks of a gradual accumulation of cells from the inferior lateral portions of the trunk as a pair of tubercular processes protruding some distance behind the ears. In *Perca* he found that these fin-pads became detached on the seventh day (No. 95, p. 10; No. 93, p. 583). The increasing density of the fin-pads is due to the entrance of mesoblast into the interstice, separating the upper from the lower epiblastic lamella. This mesoblast spreads out radially, but does not reach quite to the distal margin, and the peripheral portion remains more transparent, though the epiblastic cells which solely constitute it become columnar, and form a thickened ridge from which the fin-rays doubtless subsequently develop centripetally.* Such a mode of development as that above sketched has theoretical bearings of considerable interest. These were briefly treated in a former note (*vide* No. 124*a*, p. 697), and need not be discussed in this place further than to point out that the fin develops as a horizontal ridge, in accordance with Balfour's theory of a primitive horizontal lateral fin, and that it is independent of and prior to the formation of a girdle-rudiment. Prof. Cleland, in a paper on the Limbs of Vertebrates (No. 40), emphasised this latter point, and further showed that a limb involves two distinct elements—a radiation (*i.e.*, an appendix) and an arch, which is not a radiation, but a cincture, which always circles more or less round the body, and may be complete above or below. Prof. Cleland further stated that neither appendage nor limb-arch is the property of one particular segment,—their position being variable and their nervous supply multisegmental,—points which are

* Kingsley and Conn, in the cunner (*Tautogolabrus adspersus*, Gill), and other authors in various forms, have recognised only the lateral fins when they were defined as tubercular pads. The observers named speak of these fins as only developed when the embryo is ready to emerge—the tail being free and the capsule loosely surrounding the fish (*vide* No. 78, fig. 51, pl. xvi.). No trace of a continuous lateral fold could be seen, the fins protruding as simple outgrowths (p. 210). The extension of the thickened epiblast and hypoblast laterally is, however, a feature common to all Teleostean embryos, and a portion of this becomes defined in all the forms studied at St Andrews, and out of this defined epiblastic fold the pectoral fins arise.

supported most clearly by the development and early condition of these structures in Teleosteans.

From the primary horizontal position (*pf*, Pl. V. figs. 4, 6, 9; Pl. XIX. fig. 7), the fins change to a more vertical situation (*pf*, Pl. XIII. figs. 1, 6; Pl. XVI. figs. 6, 8), though still connected by a lengthy attachment to the side of the embryo. The mesoblast of the fin-plate may be traced to a mass of cells in which the Wolffian ducts lie, and out of which they are developed (Pl. VII. figs. 1, 2). If these ducts, as appears to be the case, arise as lateral ridges or diverticula of the somatopleure, then the mesoblastic cells of the fins must be pronounced somatopleuric. But no ridge of somatopleuric cells, comparable to the Wolffian ridge of higher forms, has been recognised in fishes, and we must regard this mesoblast as indifferent, and forming an "intermediate cell-mass" adjacent to the excretory system. The proximity of the Wolffian duct and the base of the pectoral fin is very noticeable (Pl. VII. fig. 7). The fins gradually become disconnected from the blastodermic yolk-sac, and about the time that they are free a median stratum in their mesoblast assumes a columnar character, and is seen as a transversely striated central bar in cross-section (*x*, Pl. VII. fig. 2). This plate (*x*) is gradually converted into cartilage, and extends from the base of the fin, where it is thickened almost to the distal border, at which it thins out and ceases (Pl. VII. figs. 1–3). Around this fan-like cartilaginous plate the adjacent mesoblast develops rapidly, especially near the proximal attachment to the trunk, so that a stout peduncle is formed (Pl. VII. figs. 1, 2). Viewed from above, in the living embryo, the fin appears as in Pl. VII. fig. 10, the outer and anterior margin presenting many protoplasmic processes, which seem to bind it to the epiblast over the yolk. The pigment-corpuscles, moreover, may be regularly disposed on the fin. Each fin, therefore, consists of a thickened stalk and an outspread distal expansion (*pf*, Pl. XII. fig. 6*a*), traversed from the base almost to the summit by a flattened plate of cartilage which is imbedded in a mass of indifferent mesoblastic cells, destined to become the muscles of the limb, and forming the main mass of the peduncle (Pl. VII. fig. 7). The basal part continues to become thicker, and later is disproportionately enlarged, while at the same time the more distal parts expand like a fan, and become thinner and more transparent, save where the delicate radial striations pass. The part towards the distal border in many forms quickly exhibits pigmentation, *e.g.*, in *T. gurnardus* (Pl. XII. fig. 1), *Molva vulgaris*, *Cottus*, and *Liparis*, radially disposed yellow and black pigment-spots being intermingled in the distal parts of the fin in the first-named species (Pl. X. figs. 2, 3; Pl. XVI. fig. 8), or again, rich orange stripes in *Liparis* (Pl. XVI. fig. 7).

During the third week after hatching the "rotation" of the fin has reached a stage at which its position is seen to be wholly altered, the original horizontal position (Pl. XII. fig. 1) being now exchanged for an oblique vertical attachment (Pl. XIII. fig. 1; Pl. XVI. figs. 3, 4, 7). The rotation continues until its basal attachment is almost perfectly dorso-ventral, and therefore at right angles to its primary position (Pl. X. figs. 2, 3; Pl. XV. fig. 2; Pl. XVIII. figs. 2, 10, 11). Meanwhile a pectoral bar appears

on each side of the thoracic region, extending dorsally and ventrally, forming in fact two halves of the pectoral girdle as yet disjoined below. Ryder distinguishes, before the development of the cartilaginous girdle, an oblique pectoral fold (No. 141, p. 520), consisting of a band of mesoblast, out of which, he states, the girdle develops. There appears on each side, therefore, a clear yellowish rod, tapering at its upper and lower extremities, and curved like an *f*,—as in the gurnard on the eighteenth day (*cl*, Pl. X. figs. 2, 3; also Pl. XIII. figs. 5, 6, 7). In Pl. XI. fig. 18, this bar is figured as removed from a larval Pleuronectid about three weeks old. The species was not determined. The small triangular element attached, though not unlike the post-temporal, is probably the coracoid bone. This secondary bar may be readily recognised by its form and position as the clavicular element (*cl*), and it develops in certain species, as in the gurnard, the Gadoids, and others, without being preceded by a bar of cartilage-cells, and in these forms the basal part of the fin-cartilage is greatly developed, as if preparatory to inclusion as a posterior part of the girdle. If the homogeneous, translucent, brittle rod, strongly suggestive of chitin, be the clavicle, then the elements behind, which become attached to it, must be the scapular and coracoidal portions of the permanent girdle. By the breaking-up of the basal portion of the cartilaginous fin-plate the system of basilar pieces is formed (Pl. XVII. fig. 5). Kingsley and Conn speak of this proximal cartilaginous thickening as parallel to the axis of the trunk, and as preceding the distal rays. "This basal skeleton," they say (No. 78, p. 210), "instead of appearing as a pair of rods as described by Ryder, was rather a broad plate with a central opening, as if his rods had united at their extremities." The same feature was also seen in *Lophius*. There is much obscurity in regard to the development of the ultimate elements of the paired fins, and their relation to the axial girdles. The details of this further development, with the theoretical considerations involved in their interpretation, have been dealt with by one of us in a special paper.*

Ventral Fins.—The development of the ventrals will be alluded to when describing the post-larval stages (*vide* Pl. IX. figs. 2, 3; and Pl. XVIII. fig. 3). They are late in making their appearance in the pelagic forms.

X. Methods and Technique.

I. Methods.—The ova and embryos are treated according to the usual methods of killing, fixing, staining, and cutting. Notwithstanding the large number of methods recommended by various embryologists, the ova and early embryos of Teleosteans may still be counted amongst the most difficult objects subjected to the microtomist's processes. The recommendations of various investigators are most conflicting, and a perfectly efficient and reliable killing, staining, and imbedding process continues to be a *desideratum*. Whitman, after trial of the usual hardening agents, "failed to find any completely satisfactory method of preserving the vitellus; even the germinal disc cannot well be preserved by any of the ordinary hardening fluids" (No. 159*a*, p. 152), and this agrees with the common experience of investigators.

* E. E. Prince "On the Development and Morphology of the Limbs of the Teleosts," Elizabeth Thompson Fund, U.S.A.

The plan followed by KUPFFER (HIS and BRAUNE'S *Archiv Anat. Abth.*, 1882), HENNEGUY (*Bull. de la Soc. Philom.*, Paris, 1879, pp. 75–77), and others involve too many processes to be adopted when the species studied are numerous, and the quantity of material is large.

Various circumstances conduce to render Teleostean eggs difficult objects for treatment—not only on account of their small size, pelagic ova being rarely more than a millimetre in diameter—but the tough nature of the capsule and fluidity of the contents render the removal of the former a most delicate and hazardous task. If hardened before the capsule is removed, shrinking results; and if the capsule be removed before hardening, the egg is more or less disorganised, unless the operator be very fortunate. The best sections are those gained by leaving the egg almost intact, and by hardening, staining, and imbedding *in toto*, but this plan is beset by many dangers. On removing the egg from the sea-water, and reference is made here to marine ova solely, the capsule is carefully pierced in order to facilitate the admission of the various media into which it is to be transferred. Save for this puncture, the egg is left entire, and thus it is passed through all the processes of killing, hardening, staining, clearing, and imbedding.

The paraffin method proved to be the only practical one, other methods, such as imbedding in pith, which might serve for large eggs, such as those of the Salmonidæ, were unsuitable for eggs so small and frail as those of the Gadoids, *Pleuronectidæ*, &c.* Various forms of the microtome were used in preparing the extensive series of sections of the various Teleosteans considered in these pages—the rocking microtome of the Cambridge Scientific Instrument Company being found very useful. The large Caldwell microtome, used in the classes of zoology at the United College, and kindly lent by the authorities of the University of St Andrews, was of great service; while the Jung (Thoma's) microtome was found to be well adapted for older stages of the embryos, and for adult ovaries—a series of sections being cut by Dr SCHARFF. The sweeping motion of the last-named instrument proved very efficient in cutting through the more mature skeletal and other tissues of young fishes, to which task the fixed razor of the English microtomes proved unequal—refusing, in fact, to pass through the firm connective and cartilaginous elements.

II. KILLING, FIXING, AND HARDENING—*Corrosive Sublimate.*—The saturated solution is one of the most efficient killing and fixing fluids available in the laboratory, and it kills, fixes, and hardens so rapidly that Teleostean ova require to be left in it for a very short time. As soon as the penetration of the fluid is complete, they are removed and washed in dilute alcohol, rather than in distilled water. Washing must be well done, in order to prevent subsequent deposition of crystals in the tissues. The desirability of staining, clearing, and cutting after treatment with this fluid is too well known to require any explanation—the best preparations being found to be those in which, after killing and fixing, the subsequent operations are immediately proceeded with. A mixture of two parts corrosive sublimate and one part acetic acid was found to be most serviceable. It is a powerful killing and fixing fluid, and produces the best results. For killing, two or three minutes usually suffice, and washing is then done in very weak alcohol—the alcohol being frequently changed until the killing medium is wholly extracted, and graduated alcohols follow, viz., 30, 40, 50, and 60 per cent.

Picro-sulphuric Acid (KLEINENBERG). This useful killing and fixing fluid does not produce the best results, since it frequently causes the blastomeres in early stages to expand and burst the capsule, thus entirely disorganising the embryonic structures. WHITMAN experienced the same results (*op. cit.*, p. 152), but occasionally this effect is not produced, and, if successfully killed and hardened in this fluid, ova are often found to produce most satisfactory sections. It is, however, not reliable. Creosote is added on KLEINENBERG'S suggestion, but apparently without much effect. If the ova placed in picro-sulphuric acid maintain their normal shape, they remain four or five hours, and then are transferred into 70 per cent. alcohol, which is frequently changed, as it becomes stained by the yellow picric acid. When the alcohol is seen to be uncoloured, the ova are then ready to be transferred to absolute alcohol, preparatory to clearing. EMERY recommends this fluid for

* HENNEGUY used elder-pith soaked in alcohol and covered with a layer of collodion.

hatched embryos, and it is certainly one of the best that can be used for killing and hardening them.

Perenyi's Fluid (Chrom-nitric Solution).—This fluid kills instantaneously, and preserves Teleostean ova better than any other medium tried; but in the processes subsequent to hardening, its action proves defective. The staining fluid is best added during the fixing process, borax-carmine being mingled with the solution. Pelagic eggs preserved their form admirably, and fixation was apparently most satisfactory, but staining was not very successful, and in the clearing and imbedding processes the ova shrunk, and good sections were found to be impossible. With some change in the mode of imbedding, this fluid would be most efficient. WHITMAN, however, states that he obtained good sections "more instructive than any obtained from eggs hardened in other fluids" (*op. cit.*, p. 154).

Chromic Acid.—The merits of this fluid for killing and fixing Teleostean eggs need not be insisted on. It acts perfectly; but the long washing and difficulty of subsequent staining are objections.

Osmic Acid.—Alone and in various combinations osmic acid is much recommended. The fatty elements in Teleostean eggs, however, render it a doubtful medium, and no good results were obtained. MARSHALL used it for the embryos of *Scyllium*, which were placed in ¼ per cent. sol. chromic acid and a few drops of 1 per cent. osmic acid for twenty-four hours—thence into alcohol.

Chrom-Platinum.—This mixture is said to be admirable for fixing, but WHITMAN found that embryos are often rendered brittle, and contours are indistinct. It is very slow in action, but after washing in alcohol, staining is said to be easy and successful.

Alcohol-Method.—A great number of ova and embryos were not subjected to special treatment, but were simply transferred from the tanks (sea-water) to 60 per cent. alcohol. In this they were killed and hardened, as ordinary museum-specimens are. Much distortion often resulted, yet some good sections were made of blastoderms thus simply prepared. The capsule of the egg was usually pierced with a fine needle to ensure entrance of the alcohol, stain, &c.

The graduated series of alcohols was tried, and, producing less distortion, gave fair results. The objects were transferred from the sea-water into dilute alcohol, "Dritteralcohol," *i.e.*, 33·3 per cent.; thence in 40, 50, and 60 per cent. On account of the small size of the ova, five or six hours in each sufficed, extended in the stronger alcohols to ten or twelve hours.

III. STAINING.—Only alcoholic stains were used, and Beale's solution, if not too newly made, gave very satisfactory results. It requires long immersion, rarely less than twenty to thirty hours, and is apt to be diffuse, but acidulated alcohol in a short time makes it markedly nuclear. Diluted with alcohol, the penetrative power of this stain is increased.

Borax Carmine (NAPLES formula) is one of the most successful stains—penetrating and nuclear, and sections are additionally valuable if, after overstaining, the eggs are placed in acidulated alcohol until the surplus is removed.

Hæmatoxylin (KLEINENBERG'S).—This proved less useful than might have been supposed; no good sections of early blastoderms were obtained after the employment of this stain, but more mature tissues were very satisfactorily treated, the stain being of the most pronounced nuclear character.

On the whole, the carmine stains are found to be the best.

IV. IMBEDDING.—Prior to imbedding, the ova were finally dehydrated by an immersion for two or three hours in absolute alcohol, and transferred thence either into benzine, oil of bergamot, or chloroform—clove-oil, creosote, &c., not being found to act well. The transference was made gradual by the method of GIESBRECHT. Turpentine succeeded the bergamot, in other cases a mixture of the clearing agent and paraffin followed, fragments of paraffin being added until finally the objects were transferred to pure melted paraffin in the usual way. Mixtures of the hard and soft paraffin, supplied by the Cambridge Instrument Company, were used—the proportions varying according to the temperature of the laboratory. Before transferring from the final absolute

alcohol, it was found necessary in the case of certain embryos to remove the yolk. In such comparatively large forms as *Cyclopterus*, *Cottus*, *Anarrhichas*, and *Gastrosteus*, the yolk became so dense in the hardening process that the razor of the microtome would not pass through it; hence, by dissecting off a portion of the yolk-sac, the enclosed yolk could with care be removed *en masse*. Whitman (*op. cit.*, p. 178) recommends *Gastrosteus* as especially suitable for sections, forgetful of the fact that the yolk-mass presents peculiar difficulty to the microtomist*—in contrast to the yolk-mass of more delicate ova, such as the cod, whose yolk is cut with ease by the razor. Ova which contain large oil-globules, *e.g.*, *Trigla* and *Molva*, are not reliable for cutting, the alcohol removing their constituent fluid, and leaving large empty cavities in place of the globules.

XI. Embryonic, Larval, and Post-Larval Conditions of the Food Fishes.†

Trigla gurnardus,‡ L.—In dealing with the ova of this species, it has as a rule been found at St Andrews that the ripe females are considerably larger than the males, but whether this is due to the fact that the males, as in some other fishes, *e.g.*, the salmon, become earlier mature, or to other circumstances, is at present undetermined. The rate of development of the embryo depends much on the temperature, thus ova fertilised on the 6th May hatched on the 13th day, while the embryos escaped from the eggs on the 6th day, respectively on 17th June and 5th July 1885. The spawning period of this form is thus considerable, viz., from April to June.§

The young gurnard, on emergence (Pl. XII. fig. 1), is a glassy transparent form with a considerable yolk-sac, the oil-globule (*og*) in which is conspicuous at the posterior angle, and is surrounded by a thickened layer of protoplasm (*p*). Numerous round pigment-corpuscles of a dull yellow or olive colour, often apparently dull greenish, are scattered over the head, dorsum, and latero-ventral region, but they do not extend to the tip of the tail. The dorsal margin of the embryonic fin has finely ramose, dull yellow, pigment-spots, with a few intermingled black corpuscles. These proceed within the dorsal edge, and may be traced down to the body line, a short distance in front of the tail, finally intermingling with the branched pigment on that portion of the animal. A similar pigmented area occurs along the ventral fin for a short distance. The coloration of the pectoral fin (*pf*) is very striking, an arch of pigment-corpuscles passing across the base of the organ, which, as in the young cod, is now erect. Over the yolk, as already noted, many stellate yellowish and a few black corpuscles occur, and they often anastomose. We have seen that this colouration of the yolk-envelope is characteristic of certain species, the gurnard being one, while in others, *e.g.*, cod and haddock, this feature is absent. Besides the opercular aperture, a single gill slit (?) at this stage occurs above the heart (Pl. VIII. fig. 8, *poa*),

* Wenckebach, who killed the embryos of *Perca* in corrosive sublimate, and stained in picro-carmine, alludes to this character of the yolk—"the embryos being very small, and the yolk extremely hard in the preserving reagents . . . satisfactory sections are difficult" (No. 157).

† The order of convenience only has been followed in this section.

‡ Day (*Commercial Fishes of Brit.*, p. 77) states that the gurnard probably spawns twice a year, viz., in mid-winter and mid-summer. If he means that each individual fish spawns twice, there would seem to be no structural grounds for the remark.

§ Mr Scott found ova of this species in the Moray Firth in January.

and the epidermis of the cephalic region is very uneven. The heart (*h*) has the siphonal shape, and the dilated venous end is curved to the right. In some examples a large space—Ryder's segmentation-cavity—is present below and in front of the heart (Pl. VIII. fig. 6, *pd*), while in others this space is either much reduced or is not present. In some, again, the pigment is less developed than in others, the former possibly having emerged at an earlier stage than the latter. The larva at this time hangs in the water with the yolk uppermost, the head being often directed downward.

2nd day.—On the second day the pericardial wall has, in front, shifted downward, so that its attachment terminates anteriorly some distance below the junction of the throat and the yolk-sac. The latter is diminishing, and has already receded from the rectal bend of the intestine. A large lumen is present in the œsophagus, and it distinctly passes beneath the eye. The pigment-corpuscles at the margin of the dorsal fin, which were at first amorphous, are now finely branched. A very remarkable phenomenon is the shortening of the region between the pectorals and the otocysts, coincident with the great growth of the pectoral fins. Three branchial arches are distinctly visible, and have an oblique dorso-ventral direction, but the slits do not appear to open externally at this stage.

3rd day.—On the third day (Pl. XIV. fig. 2) the chief changes are the increased prominence of the snout, which now projects in front of the yolk-sac, the general shrinking of the latter, and the very finely branched condition of the pigment-corpuscles in the marginal fin, pectorals, and on the yolk-sac (Pl. V. fig. 2*a*). More pigment, of a yellowish colour, now occurs over the mid-brain and round the eye. The reticulation of the peculiar pigment-corpuscles of the yolk-sac is conspicuous (Pl. V. fig. 2*a*), these bodies wholly differing in shape from those of the embryonic fin and other parts (Pl. XVI. fig. 8, those of the trunk being figured on Pl. V. fig. 2). The pectoral fin has acquired greater prominence, and its distal margin is rounded. Little change has occurred in the outline of the marginal fin. Surface-views still show that the oral region is impervious from the widely open mouth to the eye, but the lumen of the alimentary canal posteriorly is very distinct. The liver projects prominently opposite the posterior border of the pectoral fin. The urinary vesicle (*uv*) is elongated from above downward, and the segmental ducts often appear to enlarge before opening into it. The larvæ at this time show increased activity, and jerk or dart about at intervals, apparently for respiratory purposes. In certain cases the well formed and active larvæ keep near the bottom of the vessel, while the deformed examples float helplessly on the surface. They occasionally remain still, hanging obliquely with the head downward, and gradually descend to rest quietly on the bottom. The fine yellow pigment and shining oil-globule in the yolk are diagnostic features. The dead sometimes float as minute white objects on the surface, though generally they sink to the bottom.

5th day.—When five days old the gurnard measures ·165 of an inch. The eyes have a greenish lustre, with black pigment. The ochre-yellow pigment is now chiefly confined to the head, yolk-sac—where the corpuscles are finely ramose, the pectorals, the

anterior dorsal region, and the base of the mandible, but they are very sparse on the opercular and abdominal surfaces. In the region at the base of the abdomen black pigment-spots are numerous, while one or two occur on the tip of the snout and along the ventral margin of the myotomes. The pectoral fins form a pair of great fan-like organs dotted with yellowish pigment and very minute black spots, while delicately branched yellow corpuscles occur towards the free margin. No feature is more striking than the great development of the pectorals; they project almost at right angles to the body, their concavity being directed backward (Pl. X. figs. 2, 2*a*). They actively move with a vigorous paddle-like motion, and aid effectively in progression.

The tail now shows dorsally and ventrally three ridges which slope in the former case upward and backward, and ventrally downward and backward. The mandible remains stiff, or is very slightly movable, and as the upper jaw projects, and the mouth is wide open, the appearance produced is remarkable and diagnostic. Aeration is sufficiently provided for by this wide and rigid oral aperture, and the energetic forward movements of the fish. In a deformed specimen at this stage the urinary vesicle was large, and distended with a large number of minute highly refracting granules. Moreover, the dorsal blood-vessel (*vs*) was in course of formation, since rows of comparatively large cells formed a definite tract beneath the notochord (*n*), as was also plainly seen in the larval ling (Pl. XV. fig. 1). This specimen was apparently affected by *hydrops pericardii*, for the heart was directed at right angles from the pre-hyoidean region, and the venous portion formed a spindle-shaped process attached by a narrow neck to the ventral pericardial wall. At this latter end of the heart large rounded globules occurred, while the arterial portion was attached in front to the posterior part of the branchial framework. Probably by the dragging down of the membranous attachment of the venous end, its spindle-like form was acquired. The yolk is now very much reduced.

On the following (the sixth) day, the rapid development of pigment greatly obscured the internal structure of the young fish. On the eighth day the premaxillary region sends out a pair of prominent knobs, theprecursors of the spinous ridge which is subsequently formed. The anus, which has probably been open a day or two, now shows a distinct corrugated aperture. The rectum is often swollen, apparently with a watery fluid, and its strongly folded walls contract powerfully—expelling a riband of translucent mucus containing minute refracting (fatty ?) granules similar to that discharged in the tanks by the adult *Cyclopterus*. The mouth (*m*, Pl. IX. fig. 5) is still rigid, but widely open, and the gullet leads into a pendulous, sacculated stomach immediately behind the liver. Thus the course of the œsophagus behind the otocysts is backward and downward. The gut leaves the upper border of the stomach, passes along the roof of the abdominal cavity, and bends downward to the anus at an angle slightly less than a right angle. The whole alimentary canal behind the short œsophagus is thrown into complex rugæ, which constantly vary with the peristaltic movements of the walls. Above the cardiac end of the stomach, and surrounded by the hepatic folds, is the translucent rounded gall-bladder.

During the following days the black pigment continues to increase, especially at the base of the abdomen. At first the radiate corpuscles are separate, but they subsequently anastomose and form dense patches.

16*th day* (Pl. X. fig. 2).—The great size of the pectoral fins (*pf*) is the most prominent feature at this stage. They are in constant motion, flapping to and fro like a pair of fans, and the pigment (*pt*) on their surface is largely developed. The yellowish yolk has shrunk very much, and forms an irregular mass in the pectoral region, the oil-globule, apparently undiminished in size, still occupying a posterior position. A large vacant space (*ss*) is left in front of the rectal tract, and a similar large space (*ss*) occurs in front of the yolk. The snout is much elongated, and viewed from above is like a truncated cone just as in the adult gurnard. A feature of moment is the comparatively motionless condition of the mandible (*mn*). The marginal fin (*ef*) shows no differentiation into definite fin-areas; it is, as compared with the breadth of the body, now proportionately narrower. As above noted, the pectorals (*pf*, Pl. X. fig. 2*a*) are the most noteworthy feature, standing out almost at right angles to the trunk, and so well developed that, viewed obliquely, the young fish resembles very strikingly *Pegasus natans*. Under a lens the yellowish pigment is seen to be confined chiefly to the head, pectorals, and yolk-area. A few corpuscles occur along the margin of the dorsal fin in front, and a few also on the tail; but the body has fewer of them than previously, finely branched black corpuscles alone being present. A later stage (Pl. X. fig. 3), about three weeks after emerging from the egg, exhibits much the same features—a chitinous bar being prominent in the premaxillary region. The next stage under observation was procured, along with a large number of others, while in the Fishery Board tender "Garland," and the specimens were slightly larger than the last stage described, viz., about 6 mm. in length. They clearly were the young of the same year, as they were obtained at the close of summer, viz., 31st August. The great size of the head generally, as well as of the eyes and brain, was characteristic, and especially the broad scoop-shaped snout with the median "bite." Behind the head the pendulous abdomen projected like the yolk-sac (now almost wholly absorbed) of the earlier stages. The stomach, in fact, was found to be greatly distended with minute Copepoda, which form the staple food at this time. The pectorals are even larger than in the previous stage; while the marginal fin with its embryonic rays continues into the tail fin, which shows the notochord as a median slightly tapered axis. From this axis the rays below slant downward and backward, while those above lean upward and backward. Those coming from the tip of the notochord are short. The ventral rays are larger, and a granular opaque tract below the chorda probably indicates the site of the future hypurals. No cartilaginous rays are present. The marked downward projection of the angle of the jaw, and the lean tapering body behind the massive abdominal region are noteworthy features. As the specimens, on account of their extreme delicacy, were injured by the pressure of the water against the net, it was necessary at once to consign them to alcohol, and their colours were thus more or less lost. Large stellate pigment-spots could, however, be distinguished along

the dorsal line of the abdomen, and a linear series also passed along the ventral line of the body posteriorly. These tiny, though active and vigorous, forms, had already left the surface where their early larval life is spent, and consorted with their older brethren in the still water of the open sea at 25 fathoms. The next stage, as shown in these spirit-preparations, is about 7·5 mm. long, and the chief changes noted are as follow :—The size of the head has further increased, and the snout is longer ; moreover, several sharp spinous processes project from the occipital area, though those on the operculum are not yet much developed. The translucency of the head permits the brain to be fairly seen, and the nasal organs are clearly outlined, as well as the facial and branchial cartilages. The pectorals form large fan-like organs with pigment-corpuscles thinly sprinkled towards the tip. The rays (thirteen in number) are all united by membrane, so that the three filaments which are free in the adult must be separated later. While the proportions of this anterior pair of fins are great, the upper rays being nearly half the length of the body, the ventral fins project as mere buds, so that their use in progression is trifling when compared with the same organs in such a form as the young ling (see p. 829). Along the ventral margin at the tip of the notochord, which is not yet bent upward, three hypural elements are visible, the first being large and prominent, the last merely a thin band below the termination of the chorda. Cartilaginous rays now appear in the ventral division of the caudal, but are absent in the median and upper portions of the fin, in which embryonic fin-rays still occur. In the next stage, one or two millimetres longer (*i.e.*, 8 mm. or 9 mm.), the hypural elements have assumed a broad wedge-shape—with an even edge posteriorly and slanting from above downward and forward. Only a short process of the notochord is free, and this part is slightly flexed upward. The marginal fin still continues from the dorsum to the tail, and the inferior lobe of the latter, with its cartilaginous rays, has increased so as to constitute its greater part ; while the upper lobe, with its embryonic fin-rays, has decreased in size. The great pectorals seem to be growing, while the ventrals are also larger, and their rays are variegated with black pigment. Upon the head the spinous processes are more distinct.

When the young gurnard has reached the length of 10 mm., spines not only appear on the operculum, the angle of the jaw, and the facial surface, but attain some size, two upon the occiput being especially prominent. The long upper rays of the wing-like pectorals reach nearly half the length of the fish, while the ventrals show considerable growth, and project freely as small fins thickly pigmented with black corpuscles. Their length is not quite equal to that of the basal part of the pectorals, which are, comparatively speaking, enormous. The posterior border of the hypurals is nearly straight (in a vertical direction), and the free portion of the tip of the notochord has diminished. The small upper lobe of the tail continues to decrease, though the delicate embryonic rays are still visible in it. The remnant of the marginal fin fringing the trunk shows no cartilaginous rays.

When 15 mm. long, specimens present much the same features as the last stage (Pl. XVII. fig. 5), but the nuchal spines upon the occiput are characteristically promi-

nent. The head is large, and the body shows an evident increase in size. The first and second dorsal fins are still continuous, though their separation is indicated by an indentation. Embryonic fin-rays alone are present, those of the anterior moiety or first dorsal being short, while the longest rays occur about the posterior third of the second dorsal. This is a marked feature when contrasted with the adult, the anterior rays of whose first dorsal fin far exceed the others in length and strength. The caudal fin is more distinctly separated from the dorsal above and the anal below. Dorsally the marginal fin at the base of the caudal almost ceases behind the second dorsal, but ventrally it is broader and less distinctly separable from the anal. It still exhibits merely embryonic fin-rays. The caudal fin is somewhat conical in shape, being broad at the base and sloping to the projecting median rays, and thus very different from the slightly emarginate adult fin.

The hypurals form an almost vertical border from edge to edge, *i.e.*, dorso-ventrally, and the notochord now barely projects from the superior angle. Above the latter several linear (opaque) tracts indicate the superior accessory fin-rays, and inferiorly shorter rays appear next the hypurals. The anal fin shows fin-rays similar to those in the dorsal fin. The pectorals are still of large size, the upper rays being about double the length of the lower. The three lowermost rays that ultimately become free filaments are webbed to the tip. Black pigment has greatly increased over the fin, especially distally, and a black margin passes a considerable distance posteriorly. The ventrals now extend slightly beyond the anus. Black pigment-corpuscles have increased over the head, cheeks, abdomen, and ventral line of the body.

Frequently in this and the earlier stages specimens of a Crustacean (resembling the young of *Caligus*) are found fixed to the head or other regions by the long central process.

When the gurnard attains a length of 17 mm., the caudal fin is separate from the second dorsal, and has several accessory fin-rays. It is also free inferiorly, but the separation is marked by a gap behind which a portion of the marginal fin runs on to join the caudal, where the accessory fin-rays begin. The most prominent part of the caudal fin is still the median border; but the complete separation of the anal and dorsal fins, and the growth of the superior and inferior fin-rays, produce a great change in its appearance. The first dorsal is not quite wholly separated from the second, and its rays are considerably longer than in the foregoing stages, while the posterior rays of both second dorsal and anal are longer than the remaining rays in these fins. Black pigment is scattered over the entire surface of the pectoral fins, extending, indeed, as far forward as the border of the branchiostegal region. The lengthening of the body beyond the tips of the pectoral fins causes the latter to appear somewhat shorter. No separation of the three anterior filaments of these fins has yet occurred. The ventrals have grown slightly, and extend a little further beyond the anus. The branchiæ are now much more definitely pinnate than hitherto, and resemble the barbs of a growing feather.

At the next stage demanding special notice, the young fish measures about 21 mm.

in length, and in form closely approaches the general appearance of the adult.* The spines on the head are, however, proportionately larger. The first dorsal is appreciably larger, its supporting spines stronger, and their tips project beyond the connecting membrane, while a deposit of pigment has appeared in its median region. The posterior fin-rays of both dorsal and anal fins have increased in length, so as to cover, when depressed, most of the space intervening between the second dorsal and the caudal. A row of prominent conical papillæ, larger posteriorly, extends along each side of both dorsal fins. A series of more minute papillæ marks the lateral line. By a further development of the parts of the tail-fin at the dorsal and ventral accessory fin-rays, the outline of the tail becomes less conical, and the posterior border is now, indeed, distinctly truncated. The caudal fin is, in fact, much longer than broad at this stage. The pectoral fins, though still large, appear of less size on account of the continued growth of the trunk, as well, probably, as from atrophy of the upper or long rays. The pigment-corpuscles are, moreover, definitely grouped upon the pectorals—forming a basal and two distal bands, the latter conspicuously colouring the expanded fin. The three inferior rays are larger than the others, but still connected by membrane. The ventrals now extend considerably beyond the shorter pectoral rays. In some examples several of the parasites (*Chalimus*-stage of *Caligus*) occur on the cephalic and hyoidean regions. The pinnately fringed branchiæ show greatly increased complexity.

A specimen, 22 mm. in length, procured in St Andrews Bay, Aug. 23, 1886 (Pl. XVII. fig. 7), presents considerable increase in the pigment of the various parts, a feature probably connected with its life in the shallower waters of the bay, where the sunlight has more direct access. The pectoral and dorsal fins, and general surface of the trunk and head, are boldly marked; indeed, the little fish is most vividly tinted. Moreover, it is important to note that the three stronger radial filaments of the lower anterior border of the pectorals are now separated, and during confinement, for a short period, the connecting membrane was observed still further to disappear, as shown in the figure. Though very slightly longer than in the preceding stage, the pectoral fins are proportionately shorter, while the first dorsal and ventral are somewhat longer. The appearance of the fish, viewed from above, is shown in Pl. XVII. fig. 6.

When a few millimetres longer (*e.g.*, 24 mm.), the spines on each side of the dorsal fins, and along the lateral line, are very distinct. A trace of the connecting membrane still remains at the bases of the three free filaments of the pectoral.

Next season the young gurnards appear to reach the length of $2\frac{3}{4}$ to 3 inches in June, though others range to $4\frac{3}{4}$ and $6\frac{1}{2}$, but whether the latter and those reaching $4\frac{1}{8}$ and $6\frac{1}{8}$ inches in May are older forms of the same season, or belong to a previous one, has not yet been determined. It is probable that all may be included in the season's growth.

Gadus morrhua, L.—The ova of the cod are very abundant in many parts of the

* In a specimen whose total length was 20·5 mm. the following proportional measurements occurred:—Head, ·5 mm.; tail, 5 mm.; longest feeler, 5 mm.; trunk, 10·5 mm.; pectoral, 6·2 mm.; breadth of head, 3 mm.

sea at both surface and bottom from March to May,* and have a diameter of ·0551 inches or 1·375 mm. The embryo emerges from the 8th to the 10th day in April, and in May somewhat earlier.

Thus those which on the 16th April presented the multicelled lenticular stage with the nucleated periblast surrounding the disc, next day, at 9.30 A.M., showed a still larger number of nuclei in this zone, which, however, at 1 P.M. had all but disappeared, while the blastodermic ring had increased in size. On the 18th April the blastodermic ring extended over a third of the surface of the ovum, and two hours later it had gained the equator. At 3 P.M. the keel of the embryo had deepened, and faint indications of the optic enlargements were visible, while at 4 P.M. they were completed.† At 10 A.M. on the 19th the embryo was fully outlined, with five or six protovertebræ. The blastopore had closed, and there were traces of KUPFFER'S vesicle. At 12 noon the protovertebræ had doubled, and KUPFFER'S vesicle was more distinct. The invagination of the lens had commenced, and the alar membrane of the embryo was distinct.

20th April.—The eyes, otocysts, and mesenteron (which turns to the right) had all made progress, and the heart showed a double-celled appearance at 3 P.M. The otoliths, at first very small, occurred at 4 P.M., and the pectorals were outlined. *21st April.*—The body of the embryo jerks from side to side, and the heart pulsates languidly and irregularly (about 3 P.M.), the contractions, however, sometimes ceasing for fifteen or twenty seconds. The trunk has lengthened and the caudal extremity is flexed. The pectorals are more distinct, and the delicate processes anterior to the fins (observed in most forms) still persist. The mesenteric lumen extends as far as the heart, and enlarges in the mid-region. The notochord is now completely crossed by intermingling arcs.

22nd April.—The posterior region of the trunk and tail are now flexed, and the yolk appears to have decreased. The pectorals are well defined and pointed posteriorly, while the anterior margin is rounded. The liver forms a rounded process, the heart shows a venous end, and the pulsations are more regular (twenty-five per minute). Round chromatophores (black) have appeared on the head and dorso-lateral regions of the trunk, but they have no regular linear disposition.

23rd April.—The eyes show pigment, and that over the body has increased. Three branchial clefts and the nasal pits are visible. The violent motions of the embryos indicate their advancement, and a few issued from the eggs. The empty capsules retain their spherical shape, though a rent passes two-thirds across their diameter.

24th April.—Five-sixths of the embryos are still in the eggs. They present a similar appearance to the previous day, though the increasing complexity of the branchial region is evident, and four clefts are visible. Some of the chromatophores on the head are stellate.

* MÖBIUS and HEINCKE state that the cod in Kiel Bay spawns from January to the end of March, but in other parts of the Baltic, *e.g.* Gothland, in April; *op., cit.* p. 233 (1883).

† The temperature of the laboratory was 59° F.

25*th April.*—Further changes occur in the pectorals which are bluntly lanceolate, and in the pigment which in the eye has a bright bronze-like hue. The urinary vesicle and other viscera are advancing.

The newly hatched cod float on the surface of still water. When a current of air is directed against them some wriggle aimlessly about, others, probably less robust specimens, float helplessly in the water. The yolk-mass is often uppermost, though some of the stronger carry it inferiorly. In many abnormal forms, which have a slightly distorted or curved appearance, the yolk lies laterally on the surface of the water. Four pigment-patches diversify the transparent body of the young larva, one behind the pectorals, one towards the posterior border of the yolk, and two on the tail. The disposition of these bands of pigment is well seen when the larvæ are placed in sea-water in a white porcelain vessel (Pl. XIX. fig. 8). The larval coloration is temporary, and differs in arrangement from that in the next and subsequent stages.

27*th April.*—The free larvæ are very active, swimming forward in a straight course with considerable speed. When at rest, however, they often lie on the side, or float with the yolk uppermost. The snout has become free from the yolk-sac to some extent, and the oral aperture has burst through. The otocysts have approached the eyes. The yolk-sac is still large, but the breathing chamber anteriorly has expanded. The distinctive patches of pigment can now be made out on the trunk. In several advanced specimens the circulation was visible, the corpuscles passing along the dorsal aorta and returning after traversing about a quarter of the length of the tail.

28*th April.*—The circulation can be traced two-thirds along the tail, and though a definite branchial circulation cannot be made out, a confused movement of corpuscles having the appearance of a plexus occurs posterior to the otocysts. The larval cod swims in straight lines, and now keeps the yolk-sac inferior.

29*th April.*—The general outline is altered, the upper jaw projects beneath the eye, and a depression divides it from the olfactory enlargement superiorly. The mandible extends a little beyond the upper jaw. The yolk-sac has much diminished, the folds of the mesenteron have increased, and the branchial system become more complex, while the aorta proceeds almost to the tip of the tail.

30*th April.*—The dorsal median fin now begins over the mid-mesenteric region, and the cuticular tissues in front form an expanded cap over the head, covered with papillæ. This is the "integumentary vesicle" or "lymph-space" of Ryder, who mentions homologous structures in the Spanish mackerel and other forms. He does not now consider this as an extension of the median dorsal fin-fold, which is never carried to the front of the head. It is very characteristic of the gadoids as well as of several pleuronectids.

1*st May.*—The development of the pectorals is marked, and they are slightly angular in front, rounded posteriorly. They are brought to the sides, and by a wriggle of the tail the fish progresses.

2*nd May.*—The larval cod are now about 4·5 mm. long, and though their dis-

advantageous surroundings have diminished their vigour, they still make active forward movements, and often rest on the bottom. The yolk-sac has almost disappeared. An almond-shaped mass lies along the floor of the abdominal cavity. The alimentary canal appears to be shortened, and still shows the constriction at the pylorus. No anus has yet appeared. The urinary vesicle is unaltered.

Ryder* states that the larval cod has the integument raised above the head, and that a large serous cavity or supra-cephalic chamber is formed, which appears to serve as a float, but the latter interpretation is doubtful. The fish swims horizontally, but when at rest has an oblique position, the tail pointing backward and downward. The sub-epidermal space is very prominent in older specimens three or four weeks after emerging, and they are then very strong and vigorous, usually frequenting the bottom of the tank, a habit inconsistent with Ryder's view just stated, and shooting rapidly through the water, the large iridescent silvery eyes being the feature most readily seen. They dexterously escape from the forceps or other instrument used for their capture, and do so with considerable intelligence. The pectorals are large and strong, and the larval cod can direct its course with great agility and speed. The mandible and hyoidean apparatus project considerably, and the abdomen is hollow and shrunken (Pl. X. figs. 5, 5*a*). The lateral view resembles a Chinese caricature of a fish, or a malformed trout, such as indicated by Agassiz and Vogt,† this effect being produced by the curvature and size of the head. The anus is lateral in position, and has not yet reached the ventral margin.

It occasionally happened that favourable circumstances enabled us to rear an example to a somewhat later stage. Thus, for instance, one in which the yolk had wholly disappeared on the 31st May, though the length was only about 4 mm., presented a marked enlargement of the head, chiefly from the great increase of the hyomandibular apparatus and the projection of the angle of the jaw. Moreover, the upward slope of the mandible, so marked at a later stage, was now characteristic. When viewed ventrally, indeed, this formed a high wall on each side of the hyoidean region. The body was comparatively massive. The cephalic "vesicle" had disappeared, but the broad marginal fin still surrounded the fish, and in the tail fine embryonic fin-rays occurred inferiorly. A few also were indicated at other parts of the fin both dorsally and ventrally. Behind the now open vent a rounded margin appears in the ventral fin. The pectoral fins are very large, and show a finely radiate basal (mesoblastic) region, and a fan-like membranous distal portion. The snout in a lateral view is prominent, with a deep hollow above the pre-maxillary region. The eyes are large, deeply pigmented, and with the bluish silvery sheen so well known at a later stage. Close behind the eyes are the large otocysts with the otoliths. One of the most interesting features at this stage is the evolution of the coloration of the early post-larval stage out of the four dark bands so characteristic of the larval form. At the stage now under consideration the little cod has only two

* *Science*, vii. 1886, pp. 26–29 (fig. 1).

† *Hist. Nat. des Poissons d'eau douce*, taf. 3*b*.

well-defined bars behind the abdomen—by a partial coalescence of the dorsal and ventral masses of pigment; the others have been modified into a band of black pigment, which passes along the roof of the abdomen, and if somewhat younger forms be examined the steps leading to the coalition of the two pigment-touches are clearly demonstrated. Various black chromatophores occur on the head, at the angle of the mandible, and on the ventral surface of the abdomen. There is thus already a change of pigment, and it is easily seen how the post-larval colouration develops normally from the condition just described.

The scanty supply of suitable nourishment and the indifferent nature of the surroundings (for the water in tanks is very different from the freely aerated and healthy oceanic water) probably retarded growth to a considerable extent. Those of 4·5 mm. in length, however, were brought within a very brief distance of the forms, 6 mm. long, caught by the mid-water net in the bay.

Between the stage above mentioned and the appearance of the young cod in shoals at the margin of the tidal rocks, there has been in this country till now a blank more or less complete, only a stray specimen or two—half an inch long—having been captured in the tow-net near the surface. The observations of the last two seasons, and this with the large mid-water net,* have, however, advanced the inquiry within a measurable distance of completion. By employing the net during the winter, as well as during the spring, summer, and autumn, most of the intermediate stages were procured.

For some years the efforts of one of us have been directed specially to the elucidation of the history of the present species in its young condition, as the account given by Professor G. O. Sars for Norway was not applicable in all respects to the British Seas. In 1886, indeed, some remarks were made on the young stages of the cod, which Professor Sars had captured, at the surface of the sea, some years ago, in April amidst quantities of the "herring-food," viz., Calanidæ, *e.g.*, *Calanus finmarchicus* and *Temora longicornis*, species which abound under similar circumstances in our own seas. Besides the points indicated in the paper just mentioned it may be noted that on the 12th of June Sars found "that the clear and undivided embryonic fin surrounding the whole body had already in part dissolved into the first and second dorsal, and a small barbel was present." On the 5th of July, again, they were discovered along with young haddock, shorter and stouter in shape, under *Aurelia aurita* and *Cyanea capillata*, as well as under pieces of Algæ; and he considered that they associated with the Medusæ for the sake of the benumbed animals and the parasitic Hyperiæ. It must, however, be borne in mind that in our seas Hyperiæ (*e.g. Parathemisto*) are frequently found in a free condition and in very great numbers. Similar young cod were found at Lofoten in the stomachs of pollack (*Gadus pollachius*), shoals of which surrounded them, chased them to the surface,

* *Vide Ann. Nat. Hist.*, Oct. 1886, p. 310.

where they were thus put within reach of the gulls as well as the pollack themselves. On the 3rd August the shoals of young cod, 2 inches and upwards in length, presented the following external colouration :—Three or four parallel lines of square spots, reddish-brown and more or less bright, extended along the sides, which with the head showed an alternating silvery or golden gloss. Sars thinks that they are driven shorewards when 2 or 3 inches long, by wind and currents, and seek protection from the pollack among the Algæ at the bottom. Moreover, it would appear that the shoals succeeded each other, since they went off as they grew older. In the beginning of October, having attained the length of 4 or 5 inches, they grow more rapidly, reaching in the middle of November the length of 6 inches, while on the 10th of December they measure 6 inches to 8 inches. Towards the end of winter they decrease in numbers. Sars states that the last fishes to appear amongst the Algæ were no larger than the first, and that there must of necessity be a succession of shoals. Indeed, he describes two varieties, viz., the thickish, reddish-yellow kind, living chiefly amongst the Algæ, and swallowing large numbers of reddish crustaceans, and a second kind of a light green or greyish shade frequenting sandy ground, where the Crustacea mentioned were rare—these thinner fishes living on Annelids and young *Cotti*. Towards the end of February he followed them further out to sea, and found them measure on an average 12 inches, and he was of opinion that the "Algæ-fish" were one year old. The greatest number of these "Algæ-fish" (1 foot long) are caught, it may be noted, in summer; but towards autumn their numbers are fewer. Accordingly, Sars concluded that the "going out" takes place in the second year, and that three years, or at most four years, hardly elapse before the fishes return to their native sites as full-grown cod, ready to reproduce their species. Considerably larger fishes than the forms found in February (1 foot long) he estimated at two years old, and in these the generative elements were found at Lofoten not to be fully developed, the smallest breeding fish being nearly 1 yard in length. On the other hand, he had seen young cod 1 foot in length in the fish-market of Christiania, which had mature roe and milt.

Hitherto no very young gadoids have been captured in January, February, or March, and it is the end of April before such appear; indeed, they are more surely obtained in May in St Andrews Bay. Moreover, it does not follow that the smallest always occur in the earliest months, for some are found in May as small as any in April. The least of those hitherto secured was about 5 mm., several having been captured on the 30th April, and others of the same size on the 19th of May and 1st June. Now the little cod reared in the laboratory to a certain stage are about three-fourths the length of this on the 9th May, and though we cannot antedate the spawning period of the cod from personal observation sooner than March, there is no reason to doubt the occurrence of an earlier issue of ova and spermatozoa in some cases; indeed, the general variability would hold. This, and the differences in the rate of growth known to occur even in those spawned at the same moment, give us the somewhat wide range in size with which we are familiar in the group.

A fortunate sweep of the trawl-like tow-net on the 1st June gave a complete series of fresh specimens, from the form just described to other stages formerly seen. The smallest cod were 5 mm. in length, but they were even younger than the somewhat stunted specimens reared in confinement. They had the two post-anal bars, the sub-notochordal black band, and the scattered spots on the head and jaws; and they were further characterised by the greenish-yellow colouration on the head and snout, as well as along the dorsal region of the body, a feature so marked at a somewhat later stage; the swim-bladder (which appeared to have a short or rounded form) was distinct. The tail and marginal fin did not differ from the stage mentioned on the previous page. Almost the same remarks apply to those 6 mm. in length, some of this size presenting a pinkish abdomen from the oil of the minute copepods they had swallowed. At 7 mm. the marginal fin has many embryonic rays; moreover, the two post-anal pigment-spots have spread out, so that they form a dorsal and a ventral band, though two denser regions indicate their former condition; a median line also occurs laterally. The yellowish-green tinge is better marked.

In small forms 6 mm. long in spirit, and probably corresponding to the stage last mentioned (7 mm. when fresh), the marginal fin is quite continuous, commencing ventrally behind the well-formed anus and passing round the tail to a point on the dorsum a little in front of a vertical line from the vent, though in front of this a membranous margin projects a short distance, indicating probably a further extension of the fin. Fine embryonic rays are present throughout, except in the caudal region, where slight linear thickenings dorsally and ventrally indicate the commencement of the permanent rays. The pectorals are large, with a chimæroid base and a fan-like membrane with embryonic rays. No trace of ventrals is visible. The mandible is bent upward when closed at a little more than a right angle to the body, and the angle of the jaw is very prominent. The eye shows a notch dorsally, and a well-marked choroidal fissure inferiorly. A little black pigment exists on the snout and the top of head, and along each side of the dorsal and ventral marginal fin, while a streak also occurs in the middle line laterally in front of the tail. The same pigment appears in touches on the prominent edges of the mandible, and along the ventral surface of the abdomen.

In the beginning of May again, and also the 1st of June, similar forms are encountered, ranging from 8 to 10 mm. and upwards. The youngest of these, 8 mm. in length in spirit (Pl. XIX. fig. 2), still presents the embryonic fin from a point on the dorsum distinctly behind the vertical from the pectorals all round to the vent, the tail as yet showing no special differentiation. At points, however, corresponding to the two posterior dorsals and the two anal fins, thickenings—indications of the adult fins just mentioned—beyond the body-line are noticed, at the base of the embryonic fin. Beyond these rudiments the embryonic fin is unaltered. The tail forms a perfectly symmetrical organ, convex posteriorly, and having the notochord as a straight, tapering, and translucent streak in its centre, with the hypural and epiural elements disposed ventrally and dorsally, and so equally that the whole presents a lancet-like figure in the middle of the tail.

A little pigment exists in the interspaces of the rays over a limited area dorsally and ventrally. The pectorals have a large—almost semicircular—basal region, and a fan-shaped series of rays distally, so that they are still powerful, but the ventrals are visible only as two minute ventral papillæ on the throat in front of the former. The body and tail have increased considerably in bulk, but the head and anterior region still remain of great proportional size. The angle of the mandible is prominent, and the jaw has the larval slope upward and forward. The eye retains its great size. The black pigment occurs on the top of the head—on which the chromatophores are now larger, along the base of the dorsal, and less distinctly along the base of the ventral marginal fin, with a streak in the middle line of the body towards the caudal region. The only other pigment is in the abdominal region—from the top of the pectoral in a line downward and backward to the anus, and this for the most part is internal. Yellowish-green pigment also occurs here and there all over the surface, so that the animal when living presents a greenish translucent aspect, and it is also noteworthy that the dorsal pigment is in two sections on each side, thus indicating the two original spots. The eyes at this stage are proportionally large, as in others of the group, of a bluish silvery aspect, and with a dark arch of pigment superiorly. The bluish sheen is probably due to interference, and not to any special pigment. The abdomen has a slightly pinkish hue from the Crustacean food which filled both stomach and intestines. The branchiæ show simple papillæ.

At a somewhat older stage (Pl. XIX. fig 3) the three dorsal fins are distinct, as also are the two anal. It may be noted also that the first dorsal develops somewhat later than even the two succeeding fins, that is to say, it presents only a thickening, while they have rudimentary rays—for instance at a length of 10 mm. and 13 mm. In the latter the swim-bladder assumes a more elongate aspect. The ventrals show more evident rays, the growth of the body and head diminishes the proportional size of the eye. The snout is longer, so that the mandible bends less obliquely upward than in the previous stage. The blackish pigment has increased on the lines formerly mentioned, and also at the base of the abdomen. While in the earlier stages the tail of the young cod presents a straight notochordal process posteriorly, it now (at and near three-eighths of an inch in length) shows a distinct upward bend apparently from the development of the hypural elements inferiorly. The tapering tip of the notochord issues therefore from the upper part of the pointed central mass, the shape of the region, however, marking the usual transformation caused by the shifting of the ventral margin to the posterior region of the tail.*

A month later, viz., on the 1st June, considerable progress had been made in the growth of the young cod, which were caught both in the trawl and in the mid-water net, sunk 3 or 4 fathoms in 6 or 7 fathoms of water, showing that these fishes generally seek the lower regions of the water. The length of the smallest was about $\frac{15}{16}$

* The great length of the notochordal tip (embryonic tail) in *Lepidosteus* is noteworthy (Balfour and Parker, *op. cit.*, p. 374).

inch. The pigment is not yet arranged in transverse bars, but has the character described in the earlier stages, being chiefly grouped on the head, along the dorsum, and on a lateral line. Stellate pigment-spots are somewhat thinly dotted here and there on the sides. Moreover, in several, after preservation in spirit, the pigment-corpuscles on the head show a central nucleus, then a pale area, and externally a ring or border of black pigment, the whole presenting the appearance of minute mosaic work. The abdomen in all is tinted of a pale orange hue from the Crustacean food which distends both stomach and intestines. The same food is eaten by the small sand-eels, young armed bullheads, and other fishes captured with them. The ventrals are now well formed, and show the elongated outer rays, though these are less developed than in a subsequent stage. Glancing generally at the contour of the fish the origins of these fins (ventral) also appear somewhat further forward than in the later stages. The barbel is now distinct, though it is less conspicuous from length than thickness.

As the fishes get larger (? older) there is a distinct aggregation of the black pigment along the sides, and the appearance of a brownish tinge in the skin on which these pigment-specks rest. These young cod are paler than the young green cod, from which they are also distinguished by the size of the barbel (which is very small in the green cod), and the longer snout in front of the eye; while the appearance of the pigment-spots along the sides at once removes any ambiguity. Moreover, the eye of the green cod is somewhat larger, proportionally, than that of the cod, probably from the shorter snout, and the mandible in the former is longer, when each is about $1\frac{1}{8}$ inch in length. The cod also soon shows a series of pale dots, from 4 to 6 in number on each side, along the dorsum, and the general habit of the fish differs quite from that of the green cod, as formerly mentioned.* Spirit-specimens, about $1\frac{1}{2}$ inch long, are readily discriminated from the green cod by the pigment-bars and pale areas, and the barbel, as well as by the general sprinkling of pigment-corpuscles over the entire area in the green cod. The fins in the young cod vary considerably in regard to pigment, many presenting at this stage a slight marginal black band, but as a rule they have much less pigment than in the green cod, which, moreover, shows grains of yellow pigment in the dorsal fins, and to a less extent in the first anal.

Alexander Agassiz mentions and figures† two specimens, probably of the common cod, 20 and 28 mm. in length respectively, the former without the pigment-bars, devoid of a barbel, and with the median fins still somewhat continuous, the latter with long ventral fins, pigment-bars, and the general feature of the adult. As a rule the cod of our eastern shores show the characters of the adult before reaching so great a length. Moreover, instead of simple ventral pigment-bars, the dice-like pattern of the pigment is diagnostic.‡

The young cod which, in company with the green cod (*Gadus virens*), frequents the

* *Ann. Nat. Hist.*, Oct. 1886, p. 307.

† *Proc. Amer. Acad. Arts and Sci.*, vol. xvii. p. 286, pl. viii. figs. 4, 5, 1882.

‡ *Vide Fourth Report, Fishery Board for Scotland*, and *Ann. Nat. Hist.*

rock-pools of St Andrews in June and July, often hang in the water obliquely with their heads downward against the current. Their food at this time, when they measure $1\frac{3}{8}$ inch to $1\frac{7}{8}$ inch in length, consists of copepods, larval cirripedes, sessile-eyed crustaceans (larval), small annelids, and *Campontia*, while the green cod, in addition to that food, feeds upon minute Mollusca, *e.g.*, *Homalogyra rotata*, and various species of Ostracoda. The cod is less shy at this stage than the young green cod, and it is captured with less difficulty.

Viewed from the dorsum they have a general pale olive-green colour. The sides are iridescent, with a pretty pinkish pearly lustre. The upper surface and sides of the head to a level with the eyes are studded with dark pigment. A regular series of dark pigment-spots runs along each side of the median dorsal line to the tip of the tail. About eight dark blotches occur on looking at the median lateral line, and as these are flanked by other dark patches in the upper lateral region, they give a very characteristic appearance to the fish (Pl. XVII. fig 8). This upper lateral region, just below the lateral line, shows behind the operculum nine dark spots. The first three are continued on the silvery belly, and then cease. The rest have connections with a series of median spots (five in number) in the middle line—bands, in several instances, passing from two upper spots to one lower median, or again bifurcating inferiorly. The ventral median line has on each side a band of pigment, continuous with the bars just described; but the pigment-corpuscles are less distinct than along the dorsal lines, except opposite the base of the vertical fins, where the pigment is quite regular, and corresponds with the base of each ray. The first two dorsals have the blackish pigment towards the tip best developed on the membrane between the rays, the basal region being pale. The third dorsal has only a little black pigment. A trace of pigment also occurs towards the commencement of the anal fin. Blackish pigment is scattered on the sides and under surface of the mandible, and a thin dark streak passes backward in the middle line. The eyes are of a pale olive-green hue, with dark specks of pigment. The upper opercular region, and the surface above the cerebellum, are of a pale pinkish colour, due to the blood-vessels and the brain beneath. The vascularity of the latter seems to be considerable. The opercular region and the body are silvery. The pointed teeth are very evident in the jaws.

The later stages have been dealt with in former papers, and need not be alluded to at present, except in regard to Eimer's* notion that the markings in animals are primitively longitudinal. Now the young cod is conspicuously speckled in its earliest stage, and is rather pale and translucent in its next condition, the pigment which forms the transverse bars gradually grouping themselves on a somewhat pale surface, without a trace of longitudinal bands. In many other fishes, both round and flat (Pleuronectids), the same arrangement obtains, so that Haake had good grounds for demurring to this view from the study of the Australian fish *Helotes scotus*, which in the adult is marked by eight longitudinal bands, while young specimens have in addition a row of clear

* *Zoolog. Anzeiger.*, viii., 1885, pp. 507–8.

transverse bands which disappear when they attain maturity. In one fish, viz., the ling, the post-larval stage is uniformly tinted, the next stage longitudinally striped, the third transversely barred, while in the adult it is uniformly tinted as in the older post-larval condition. No rigid rule can thus be held.

Gadus aeglefinus, L.—The ova of the haddock are about ·058 in., varying a little, *e.g.* from 1·65 mm. to 1·5 mm. The development of the embryo ranges from six days in June to twenty in March.* Thus a series received from Granton presented on the second day (22nd March 1885) a blastodermic cap ·4 mm. in diameter. It reached the equator on the fourth day. While the keel of the embryo indents the yolk, the head is defined, and everywhere shows further progress. On the fifth day the optic enlargements are distinctly outlined. Faint indications of protovertebræ (four to five in number) appear in the anterior caudal region, and scattered black pigment-specks show on the sides and dorsum. On the seventh day, at 9 A.M., the blastopore had closed, but KUPFFER'S vesicle was not apparent till next day. The lenses of the eye are fully formed, and the heart is represented by a granular patch. On the tenth day the various regions of the brain were defined, with the nasal pits, the otocysts, and an opercular cleft; the liver is indicated on the ventral aspect of the alimentary canal. No cavity is visible in the heart; the latter pulsates on the eleventh day about ten times per minute, though occasionally a little more rapidly, and shows a somewhat triangular cavity.

The pigment-spots are more numerous and more elaborately stellate on the twelfth day, especially on the dorso-lateral regions above the pectorals. A lateral fold arises behind the latter and passes along each side. The lumen of the mesenteron has notably enlarged next day on the dorsal side of the liver, but it diminishes very much as it approaches the cephalic region. On the fifteenth day the cephalic region has increased in size, and the body has considerably lengthened. Embryonic rays have appeared in the marginal fin. The heart pulsates on the seventeenth day about thirty times per minute. The eyes have a punctate appearance from the development of pigment, and the first branchial cleft is distinct. On the eighteenth day the eyes have black pigment. A second branchial cleft occurs on the ventral side of each otocyst. The liver has largely increased and projects into the yolk-sac. The pectorals show a distinct rim. The alimentary canal is filamentary anteriorly, and ends blindly in an enlargement posteriorly. Three branchial clefts are visible on the nineteenth day, and the pulsations of the heart are forty per minute. A buccal chamber is continuous with the mesenteron, which has a flexure to the right of the embryo. The segmental ducts and the urinary vesicle are well advanced.

The embryos emerged on the twentieth day 3 mm. in length, and with a yolk-sac ·5 mm. in its long diameter. They attempt to progress with the yolk-sac downward, but at rest are inverted. The black pigment-corpuscles are grouped somewhat densely behind the otocysts, and extend backward a little beyond the commencement of the

* In contrast with the ova fertilised on the 24th April, and hatched on the 3rd May—that is, in nine days.

intestine. A line of the chromatophores passes along the infero-lateral region from the beginning of the mesenteron to near the caudal tip, and a few exist on the dorsal part of the abdominal region. A fourth branchial arch is visible. A delicate polygonal protoplasmic meshwork occurs over the surface of the yolk, as in the flounder. The walls of the heart are thinner, and cellular strands pass backward to the liver. There is neither mouth nor anus. The alimentary, renal, and other organs have been further developed on the third day (of freedom), and the urinary vesicle sends down a fine strand of cells, the precursor of the urino-genital tube. On the fifth day rapid elongation of the skeletal elements of the mandible has occurred, the head has been raised, and the cranial flexure diminished. The point of the snout is now in the same line as the ventral margin of the liver. The abdominal pigment has increased, but there is little change in the rest. The oral chamber has now burst through. The otocyst presents a ridge growing up from the floor, and a chamber descending from the roof, the otoliths lying on each side of the former. A lenticular mark indicates the anterior nares. The mouth gapes, but only erratic movements of the parts take place. Next day the mandible protrudes further, and the branchial and hyoidean arches are prominent. The yolk-sac is oval and much diminished. On the seventh day blood began to pass into the heart, but the death of the embryos arrested further examination.

The newly hatched larvæ of this species are very small, about 3 mm. in length, and irregularly pigmented with black. They emerged in June, in about six days after fertilisation, and are very active when free. In a week they are difficult to see when resting on the bottom, and if stimulated they glide rapidly, seldom rising above the bottom, or at any rate rising very little, and progressing with a jerking motion, the yolk-sac being inferior. When at rest in the water, the head hangs slightly downward as in other young fishes, and in descending they wriggle a little and elevate the anterior region. They are chiefly recognised by the eyes, which are large and pigmented, and also by the pigment passing along the dorsal edge of the abdomen as well as a faint line below the muscle-plates of the same region.

The post-larval stages of the haddock have hitherto escaped detection, and it is only when the fish reaches the length of upwards of 2 inches, with the characters of the adult fully displayed, that it has come under notice. Few authors allude to the very young stages of this form, though G. O. Sars thought he could distinguish them amongst other young gadoids by their shorter and stouter form. Collett again states that he found the young haddocks 7 cm. long under *Cyanea capillata*.*

Gadus virens, L.—The ova of this species have not been recognised in the ripe condition. It is stated by Kröyer to spawn in January. In its earlier stages the green cod probably resembles the cod very closely, and follows similar habits. When $1\frac{1}{8}$ inch in length they come in large numbers to the margins of the tidal rocks about the end of

* *Vide* Möbius and Heincke, who quote without criticism the remark of Malm that the haddock spawns in shells on the west coast of Sweden from January to March; and that in the museum at Kiel is a shell-fish on which are ripe eggs.

May and beginning of June, preceding the arrival of the young cod of the stage formerly mentioned, though perhaps not always. The characteristic features of the species, as distinguished from the cod of the same size ($1\frac{1}{8}$ inch), have already been indicated. They consist of a deeper green hue all over, but especially anteriorly, and a much greater development of black pigment-corpuscles both on the body, head, and fins. The eyes also have a greenish hue, and these are proportionally larger than in the cod. The fins throughout are duskier from the black pigment, and the three dorsal and anterior anal are often marked by yellow pigment-grains. The pectorals in some show traces of two broad arches of pigment, after the manner of other larval forms, such as the gurnard and armed bullhead, though much less distinctly. The ventrals are well formed but small, and show no special elongation of the outer rays. When specimens of this and the cod are viewed side by side from the dorsum the difference in regard to pigment is striking, the green cod being almost uniformly pigmented from the tip of the snout backward, whereas the cod shows such chiefly on the tip of the snout and over the brain. Moreover, the snout in the young cod is decidedly longer and narrower, so that with the distinction already noted in regard to the size of the eyes the whole facies differs. In profile the gape of the cod is the longer, the mandible apparently being longer, and the angle more pronounced.

A curious feature was observed in those killed by a few drops of corrosive sublimate (in acetic acid), viz., the closely adpressed condition of the first dorsal fin.

In somewhat older forms, which are abundant in the rock-pools in July and August, two varieties occur, viz., one of a pale though dull green along the dorsum and upper lateral regions, the other of a dark olive-green in the same parts.*

Gadus merlangus, L.—The eggs of the whiting abound in April and May, and probably later.† They measure ·0476 in., or about 1·125 mm. In an instance in which they were fertilised at 3.30 P.M. on April 15, 1885, the germinal cap was found at 6 P.M., and forty minutes afterwards the first furrow had appeared. At 9 P.M. segmentation had proceeded beyond the eight-cell stage, and soon sixteen were outlined, the nuclei in these being apparent at 9.40 P.M. On the second day, they were in the multicelled stage, but no well-defined nuclear zone was visible, the latter being very distinct on the third day. The blastoderm had largely extended on the fourth day, and on the sixth the blastopore had closed, though KUPFFER'S vesicle had not yet appeared. Lenses and otocysts were present. No pulsations of the heart occurred early on the seventh day, but later intermittent contractions took place. Finely stellate chromatophores develop on the yolk-sac.‡ On the eighth day yellowish chromatophores appeared on

* *Report on Trawling* (1884), p. 360.

† DAY says the whiting "spawns in March not far from the shore," though what advantage the latter situation gives is not stated. MÖBIUS and HEINCKE observe that, according to BENECKE, it spawns on the Prussian coast from December to February, and in the Cattegat, according to MALM, from March to May.

‡ Mr CUNNINGHAM considers that in the larval whiting the chromatophores are confined to the body of the fish, and are absent from the marginal fin and the surface of the yolk. His diagnosis rests on specimens captured in the tow-net (*Jour. Mar. Soc. Biol. Assoc.*, N.S., i.) In our experience the whiting is a form very early characterised by its yellowish pigment, which invades the marginal fin.

the dorsal region, and on the yolk-sac, near the trunk. The cardiac pulsations were vigorous and regular. The pectorals were distinct. Next day the movements of the contained embryos were active, and some emerged at 5 P.M., most however issuing next day (tenth after fertilisation, viz., 24th April): they are delicate, translucent forms, and swim vigorously near the surface. The pigment is characteristic (see p. 126).

The oldest larva reared in the laboratory is shown in Pl. XVII. fig. 12. It is distinguished by its black pigment-spots arranged in a double series along the edges of the muscle-plates, the inner row in each case being somewhat fainter. Dorsally the outer row reaches forward to the mid-brain. A dense pigment-band exists in the subnotochordal region of the abdomen. Scattered spots of considerable size occur on the mandible, over the cardiac region, and on the ventral surface of the abdomen. As in many other forms the dark pigment abruptly ceases in front of the caudal region. The yellow chromatophores are distributed generally over the head, trunk, and fin-membranes. The eyes are bluish silvery, the snout is still blunt, and the mandible is stout and prominent. The subepidermal serous space over the head is well marked, and extends as far as the anal region. Three sensory organs are present in it. The otocysts are comparatively large. The blood-corpuscles are distinct. This example nearly bridges the gap to the post-larval forms. At this stage the great translucency of the species is noteworthy, all the organs being most clearly observed.

The earlier post-larval stages of the whiting, viz., those immediately following larvæ reared in the laboratory, are still somewhat obscure, though they probably closely approach those of allied forms, such as the cod and haddock. The characteristic nature of the larval pigment, however, would lead to the belief that in the brighter colours (*e.g.*, yellow) early differences may occur. Such, as a rule, were lost before they came under observation; for all these delicate forms are dead and considerably altered before reaching the deck, and the same remark applies still more decidedly to those immersed in spirit. The pressure to which they are subjected in the large mid-water net, by the currents, and by the weight of crowds of Appendicularians, Medusæ, and Hydromedusæ, as well as Ctenophores, would alone sufficiently explain this; nor are these dangers obviated by the use of large wide bottles at the extremity of the net.

So far as present observations go, the young whiting appears to be recognisable as such when from 9 to 12 mm. in length, examples of these stages occurring in August (1886). The dorsal, anal, and caudal fins have permanent rays, and the several parts of the two former are all outlined but not separated from each other. The pectorals form large fan-shaped organs, but the ventrals are minute. Groups of black pigment-corpuscles occur on the brain and along the sides of the dorsal and anal fins, while a line runs in the median ventral region of the abdomen. The sides of the body posteriorly have a more general sprinkling of black pigment than in the cod, which, however, it closely approaches. No barbel is noticeable.

When about 15 mm. long the species is distinguished by a more abundant covering of minute black pigment-specks along the sides of the body and on the fins than in the

cod, and by the greater length and diminished depth of the first anal fin. The pigment-specks are still present in the median ventral line of the abdomen. These characters are better marked at 18 mm., the black pigment-lines at the bases of the anal fin-rays being especially characteristic when contrasted with the young cod, in which a median line of black pigment proceeds from the centre of the tail forward to a point above the middle of the first anal. No barbel is present, and the myotomes are more closely arranged than in the cod.

At the length of 20 mm. the first anal of the young fish assumes the adult characters, and a small papilla now indicates a barbel. The pigment along the dorsal edges is much more developed than along the ventral. The general and minute flecks of black pigment are very characteristic at 24 mm., and the barbel has increased in size. The denser dorsal pigment, moreover, has spread downward over the sides, but in the preparations is uniform; and no dappled condition was noticed when fresh.

Between the foregoing and a length of 28 mm., a decided change takes place in the region of the pigment last mentioned, viz., a tendency to form separate touches along the dorsum, somewhat after the manner of those in the cod. These dark touches are confined to the dorsal region, though in some a few bars occur at the base of the tail. The fish is now minutely flecked with black pigment all over the sides, head, snout, and fins, a few large corpuscles appearing in the dorsal and the hyoidean regions—the silvery sides and under surface of the abdomen alone being free from them. In general outline it approaches the adult. The shortness of the snout readily separates it from the cod—without reference to the first anal fin. A slight duskiness exists above the base of the pectoral, but no definite spot. The tips of the ventrals reach fully to the vent. The row of pigment-spots usually disappears from the median ventral line at the length of 30 mm. The barbel is small but distinct at this stage.

The young whiting at 34 mm. presents the following features when contrasted with a cod of the same length (in spirit). Externally parasitic *Caligi* are generally more abundant in the cod. The median dorsal fin is less abruptly elevated than in the cod, and the first anals diverge widely. The body of the whiting is more neatly rounded and more plump than that of the cod, which often has a protuberant abdomen. This outline in the whiting is probably due to its earlier maturity. Though a smaller fish it issues from an egg somewhat larger than that of the cod. The pigment-specks closely cover the sides of the body of the whiting and the membranous webs of the dorsal fins. The same pigment is continued forward on the head. The pigment at the bases of the caudal rays is more distinct in the whiting, and the lancet-like caudal termination of the body is longer in this species. Moreover, the myotomes are coarser in the cod, and the surface has little of the dappled silvery sheen of the whiting, apparently from the somewhat more advanced condition of the scales in the latter. The finely stellate black pigment-corpuscles are larger in the cod, and instead of the general specks of the whiting, they are grouped in blotches over the surface, with intermediate pale regions, and the head and neck are much less covered with pigment. Both pectoral and ventral fins of the

cod are shorter than those of the whiting, the tips of the latter leaving a considerable interval between them and the anus. This abbreviation of the abdomen coincides with the very long first anal fin, and is as characteristic of the adult as the young. The snout of the whiting is shorter and broader than that of the cod, and its depth is greater. The long barbel of the cod contrasts with the short process in the whiting.

At 54 mm. the pigment has increased, and the elongate tips of the ventrals pass beyond the anus. The barbel is distinct but small. It is interesting that no young whiting of this and previous stages has been seen without a barbel, yet Mr Day and other authors do not allude to the subject, apparently considering that the young agree with the adult forms in this respect. Young whiting, between 3 and 4 inches in length, have more than once been observed with a distinct barbel, indeed, a stronger statement may safely be made, viz., that at $3\frac{1}{2}$ inches some present the barbel, others do not.

The Ling (*Molva vulgaris*, Flem.).—The ova of the ling measure ·066 to ·0916 in., or about 1·08 mm., the oil-globule being $\frac{4}{15}$ of that size. They were fertilised at sea on the 27th April,* at 12 noon. When received at the laboratory at the forty-eighth hour, they were in the biconvex morula-stage. They appear to be more delicate than the ova of the cod and haddock, and many were collapsed, the contracted globe of yolk carrying the oil-globule in its wall of protoplasm away from the inner surface of the zona radiata. The nuclei of the periblast were about one-third the diameter of the blastodermic cells. The zona is not so soft and tough as in the cod and haddock, but shows greater resistance, bursting rather than collapsing under pressure.

Third Day.—About a fourth of the yolk is covered by the blastoderm, and the rim is broad and distinct. On the following day three-fourths of the yolk are enveloped, and the shield is outlined; some show metameric segmentation in the middle region of the trunk. In the median line of the body are a number of clear protoplasmic vesicles between the embryo and the yolk-surface. In many, the blastopore is closing, the optic vesicles are contracted off, and the notochord ends abruptly in the pectoral region, but terminates indefinitely at the caudal end; fifteen or sixteen somites can be observed, but the three regions of the brain can barely be discerned. The envelope of the yolk (blastoderm) is dotted with pale neutral-tinted corpuscles of various angular shapes which send out processes. The blastoderm shows a double contour (probably epiblast and hypoblast) as it passes off on each side of the embryo.

On the sixth day the lenses are in process of formation, but cannot be fully made out. The neurula is well defined in the cranial region and has a marked keel. The large cells of the closed rim of the blastopore persist at the posterior end of the fissure between the embryo and the yolk. In other Gadoids, these have generally disappeared at this stage. The blastodermic shield is reduced to a mere film on each side, but the peculiar fan-like mass of cells and protoplasmic threads in front of the pectoral region (as in other species) has larger and more definite cells than usual. The clear corpuscles of a neutral tint scattered over the yolk near the oil-globule are still present.

* The ling is said to spawn on the Skagerrack in May.

Rudely stellate (*i.e.*, with short rays) black chromatophores appear on the seventh day (May 4), on the dorsal surface of the trunk. The vesicles on the ventral surface still persist along with KUPFFER'S vesicle. About thirty somites are visible, and the caudal plate rises prominently upon the yolk. The otocysts are also present and have a circular outline. The heart is being differentiated from a protruding mass of cells below the otocysts, and folds immediately behind indicate the mesenteron. The oil-globule projects from its pocket in the yolk, externally having a covering of blastoderm. A central fissure occurs in each eye.

Eighth Day.—The tail is well formed and is laterally flexed on the yolk. The finely branched chromatophores form two somewhat regular dorsal lines, and five or six solitary spots also occur over the yolk, in its outer envelope. The cardiac pulsations are faint. The nasal bulbs are distinct, and the lenses of the eyes fully formed. Very delicate round pigment-spots of a pale greenish-yellow colour appeared about noon, giving the ovum a slightly greenish tint to the naked eye. These greenish-yellow corpuscles were thickly scattered at the ventral margin, and especially on the marginal fin, almost to the tip of the tail. Each segmental duct ends in a space above the end of the intestine, and the anal tract sends a protoplasmic tube partially across the tail-fin. The lumen has an external opening on one side of the caudal fin-membrane.

Next day (6th May) the embryos (Pl. XIII. fig. 4) emerged, though some which had been isolated in a small quantity of sea-water in a room escaped the previous day. They measured about 3 mm., the yolk being 1 mm. in its long diameter. They appeared to be delicate, many lying on the bottom, while the more active floated in the reversed position near the surface, and were able to wriggle a little. The liver appears to be further back than in the other Gadoids examined, the distance being nearly one-fifth the length of the head and trunk (excluding the tail). The fine lumen of the mesenteron extends to the opening formerly indicated. Anteriorly it ends as a fine fissure behind the heart. About fifty myotomes are marked off, and the caudal trunk terminates in a slight enlargement. The otocysts have thick walls, and just in front of them are two clefts. The heart slowly pulsates. The finely stellate chromatophores in the caudal region seem to correspond in number to the lines of the metameres.

The larvæ on the 7th May presented certain peculiarities at the tip of the notochord very distinctly, viz., a slight enlargement followed by a constriction, then a large swelling in front of the terminal knob. The lumen of the intestine was slightly increased, though still smaller than the mesenteron proper. The urinary vesicle (which communicated with the rectal portion of the canal) showed continual movement of its walls. The yolk-cortex has receded considerably from the outer envelope (blastoderm) leaving a large extra-vitelline space, and the oil-globule (*og*) is also lifted away from the outer layer. The distance of the heart and the oral region from the liver is still marked. The heart, on the 8th May (Pl. XVII. fig. 9), was much flexed, asuming an S shape, but no definite wall to the pericardial chamber was visible. The yolk has diminished. On the 10th May large ramifying chromatophores occur over the yolk,

their long zig-zag processes being characteristic. Two or three extend over the whole yolk-surface. The larva now measures $3\frac{1}{5}$ mm.; from the snout to the anus $1\frac{1}{10}$ mm., the tail being thus very long, viz., $2\frac{1}{10}$ mm. The lower lobe of the caudal fin appears to be larger than the upper. The envelope of the oil-globule is thickened, and pigment appears in it. The greenish-yellow pigment-corpuscles are more numerous, and have a well-defined oval outline. These corpuscles are clear and homogeneous in vigorous examples, but they become granular in moribund and decaying forms; moreover, while the black chromatophores are elaborately stellate these remain amorphous or rounded. The larval fishes shoot upward from the bottom of the vessel, and strive to reach the surface with more or less success, then, hanging head downward, sink slowly to the bottom. In their upward course the yolk-sac is inferior, but when the fish is motionless it turns uppermost and the fish descends.

On the sixth day after emergence (12th May), an indentation passes across the nasal region, but in the earlier part of the day the mouth is not yet open, though a fold of epiblast hangs like a curtain on each side. Later in the day the mouth appears as a lenticular slit, cells defining its upper and lower margins.

At the end of the first week of freedom (13th May) the larval fish measures $3\frac{3}{10}$ mm. (Pl. XVII. fig. 10). The mouth is freely open. The eyes are deeply coloured with black pigment. An opercular fold has grown over the cleft, leaving a fissure behind and below the otocysts, which are now spacious and thin walled. The pectorals still have a horizontal attachment, but can be elevated and depressed; and they show radial thickenings (fin-rays). The yolk has much diminished, and has five or six large stellate black chromatophores, but these do not extend beyond the yolk proper (in the cortex), whereas the yellow spots occur all over the integument. A pericardial wall appears, and the endocardial surface is rugose. The anus now opens (?) on the lower margin of the fin, and the space between the anus and the oil-globule is large, as the latter has been dragged forward by the wall of the diminishing yolk, but the globule itself does not appear to be much smaller. Large black chromatophores occur over the mid-brain, and a row of them begins near the root of the pectoral, and extends along the dorsal region, ceasing above the anus. At the latter a line commences along the upper margin of the notochord and ends a short distance from the tail, extending over $\frac{2}{3}$ of the caudal trunk. At its termination, a confused mass of elongated chromatophores trends from the margin of the muscles outward over the tail-fin. A similar mass passes ventrally. A concentration of black pigment also occurs on the dorsal surface, behind and above the otocysts.

On the 30th August 1886 very young examples of the ling (Pl. XVIII. fig. 3), about 8·5 mm. to 9 mm. in length—resembling *Phycis*, were captured. Along the dorsum a slightly greenish tint was observable, with minute scattered black pigment-spots. Two well-marked black bars pass behind the abdomen, one a short distance posterior to the latter, and another in front of the base of the tail. They are best developed ventrally, and do not reach to the dorsum, while a pale brownish hue surrounds them. Under the

anterior end of the mandible as well as on the summit of the head black spots occur. A most striking feature is the extraordinary length of the ventral fins (*vf*), three of the fin-rays in each being very long, while the fourth is shorter. The fins are of an ochre-yellow colour along the rays, with specks of black pigment scattered over the inter-radial membrane. The iris, like that of the eye of the whiting, is of a pale sky-blue. The notochord passes almost in a straight line backward to the tip of the tail, and the caudal fin is continuous with the unbroken marginal fin dorsally and ventrally. The great development of the ventral or permanent rays, however, slightly pushes the tip with the embryonic radial striations upward. The hypurals, two of which are very distinct, are developing inferiorly, and the epiurals dorsally, but they have only slightly affected the direction of the notochord. The early development of the upper caudal rays in this form is of interest, as it is in marked contrast with such forms as the Pleuronectidæ in which the inferior fin-rays alone appear.

The head and the eyes are disproportionately large, and the prominence of the hyomandibular apparatus, as well as the size of the mandible, gives to the jaws a massive character, just as in the cod. The angle of the jaw is especially marked, projecting prominently inferiorly—rather behind a vertical line drawn from the centre of the lens. The hyoidean apparatus, and subsequently the whole facies, the opercular structures, and branchiostegal rays, are remarkably developed. The pectorals (*pf*) have short fleshy bases with fan-like expansions of fin-rays of moderate length, not unlike the condition in the adult. The barbel can barely be distinguished. The alimentary canal has a comparatively simple course, the capacious stomach bending to the right, whence a wide and straight intestine passes backward nearly to the anus, then bends forward, doubling again behind the stomach on the left side, before proceeding straight to the anal opening.

The next observed (on 21st July 1887) was about 15 mm. in length, three occurring in the mid-water net in a haul at 22 fathoms. The pigment and other characters of these do not require special mention. The yellow pigment is at once removed by alcohol, but the black remains.

On 31st August 1886 examples of the next older stage (Pl. XVIII. fig. 4) were obtained off the Isle of May. The dorsum again was greenish, and a similar pale tint existed over the trunk and tail, while along the sides of the latter black pigment occurred. The long ventrals extended more than one-quarter the length of the body, three rays being especially distinguishable for their size, while three rudimentary rays were present at the base. Their colour is similar to that of the last stage. The pigment of the body, especially that of the two black bars above described, is now more diffuse and continuous, the bars being however indicated by two isolated dorsal bands. The blackish pigment in front of the ventrals is more definite, forming a broad arrow or Λ-shaped figure, and at the tip of the mandible, on each side of the symphysis, a band occurs, and a trace also is distinguishable in front of the barbel. Dorsally, a slender stripe exists along the premaxillæ, and the pigment on the cranium is better defined. All these external features were, however, already indicated in the younger examples.

At this stage the ling measures about 20 mm. in length, and the differentiation of the first dorsal is complete, its position being as in the adult. The relations of the second dorsal fin are similar, as is also the case with the anal and caudal, the approach to the adult condition being marked. The tail, however, is more ovoid in shape than in the adult. The pectorals (*pf*) are broad dorso-ventrally, while the ventrals appear to be less advanced, that is, more directly under the pectorals than in the adult. The development of the hyoidean and opercular structures alters the outline of the angle of the mandible. At this stage the parasitic young *Caligi* also occur on the ling.

The next stage observed was a specimen $3\frac{1}{2}$ inches long, which had been stranded in a pool on the sands in the middle of December.* The fish is now boldly striped longitudinally; thus an olive-brown band passes from the tip of the snout in a line with the middle of the eye straight backward to the base of the caudal fin-rays. The pale ventral surface bounds it inferiorly, while dorsally a stripe with a beautiful opaline lustre runs from the tip of the snout over the eye backward to the base of the caudal rays. The latter band is opaque white on the tail, and it gives the fish a characteristic appearance. The dorsal fins are well marked, the first presenting a distinct black speck posteriorly, and another black pigment-patch occurs at the end of the last division. The dorsal line from the brain backward is distinguished by a narrow edge of dull orange or pale olive, and this brings out in relief the colours formerly mentioned. The little ling is thus a longitudinally striped form, and in strong contrast with the tessellated condition of the young cod. The barbel is proportionally large, and is borne by the fish horizontally, *i.e.*, projecting in front of the snout.

At a later stage, viz., from 8 to 9 inches in length, when it abundantly frequents the rocky margins, the ventrals show three free filaments, the first shorter than the second and third—which are nearly equal. These filaments in the previous stage (3 inches) are worn off in confinement, indeed all the fins are frayed. The change which ensues at this advanced stage has been formerly described by one of us,† and may be summarised in a specimen $7\frac{3}{4}$ inches long as follows:—The fish is now boldly and irregularly blotched with brown, both dorsally and laterally, the region of the white stripe being indicated by the pale and somewhat scalloped area dividing the lateral from the dorsal blotches. Fourteen or fifteen of the latter occur between the pectorals and the base of the tail; they are separated by the whitish areas, which thus assume a reticulated appearance over the anterior dorsal and lateral regions, and both kinds of pigment invade the dorsal fins. The original dark greenish band is more or less evident from the tip of the snout to the posterior part of the operculum, but thereafter it is lost. The tail has a pale border, with a dark brownish belt of considerable breadth, and a few black touches in it. A broad white streak exists in the upper half within this, but is feebly marked inferiorly. The black pigment is largely developed in the

* *Third Annual Report, Fishery Board for Scotland*, p. 62, 1885. Another example of the same size has since occurred in March.

† *Fourth Annual Report, Fishery Board for Scotland*, p. 209.

brownish belt along the inferior margin. The black spots on the posterior part of the first and second dorsals are very distinct, and the dark belt of the anal is densest at the posterior end. In life the whitish streaks often have a bluish appearance.

The remarkable length of the ventrals in the post-larval ling resembles the condition described by Alex. Agassiz, in *Onus*,* and in *Motella*.

Motella mustela, L.†—The ova of this species abound in the sea from March to May, and those in the tanks shed their ova freely in April. The unimpregnated egg on its escape has a diameter‡ of ·73 mm., the measurements given by Mr Brook (No. 31) ranging from ·655 to ·731 mm. The hyaline capsule is slightly corrugated, and the entire yolk-surface presents a series of minute oleaginous particles. Mr Brook's larvæ emerged on the fifth or sixth day, but at the laboratory the development was less rapid at the beginning of May, probably from the much colder surroundings. Thus ova, in which the blastoderm had enveloped two-thirds of the yolk (probably more than three days after impregnation) on the 4th May did not emerge till the 11th May. Nine proto-vertebræ were visible on the 5th, and the blastopore closed on the 6th May. The optic vesicles were well defined, but the otocysts did not appear till 5 P.M. of this day, the first sign of their cavity being a very fine slit. Brook gives the length of the newly hatched larvæ at 2·25 mm. About the sixth or seventh day after hatching the mouth resembles that in the young plaice, the lower jaw projecting very much (Pl. XVII. fig. 2). An oil-globule occurs in the small portion of the yolk still remaining. The marginal fin is finely fibrous, and in the caudal region fine threads stand out in the moribund animal. The notochord shows very large cells, those in the tail being rounded and forming a single linear series, while the anterior are smaller, more numerous, and irregular. An interesting condition of the termination of the neurochord is seen at this time, for it exhibits a distinct lobular dilatation (*ne*) having a fine central canal (*nc*) which can be traced a long way forward. This terminal nervous enlargement (*ne*) projects beyond the end of the notochord (*nc*) (Pl. XV. fig. 4). The skin has a very irregular surface many from granular papillæ. Three days later (May 11th) most of the embryos had died, as they are somewhat delicate forms; but the survivors (see fig. 2, Pl. XVII.) show a beautiful iridescent area behind the pectoral fins, probably from the swim-bladder. The yolk-mass has been absorbed and the median dorsal fin has diminished. The mandible (*mn*) is still prominent.

Proceeding to consider what may be called the post-larval stages, procured in St Andrews Bay, we note that Alex. Agassiz,§ in one of his papers on the young stages of "Osseous Fishes," in which he made known the remarkable development of the ventrals in a form doubtfully regarded by him as a *Motella*, speaks of it as *Motella argentea*, Rhein., though he added that it might be a species of *Onus* described by Collet.

* *Op. cit.*, p. 273.

† The egg and larval form figured by Mr Cunningham (*op. cit.*, p. 105, pl. vii. figs. 3, 4) evidently belong to *Motella*.

‡ In parts of an inch their diameter is ·0283, and the oil-globule ·0033 or less.

§ *Proc. Amer. Acad. Sci. and Arts*, vol. xvii., July 1882.

There is no uncertainty, however, with regard to the genus of the form about to be described. It is clearly a *Motella*, though more probably *M. tricirrata* than *M. mustela*.

The youngest stage captured in the large mid-water net at the end of August is 6 mm. in length (Pl. XVIII. fig. 6), and the embryonic fin (*ef*) is still connected with the base of the tail both dorsally and ventrally, the specimen being apparently about the stage of Agassiz's, pl. vii. fig. 6. The body of the British fish is, however, proportionally shorter and deeper. The head is large and the snout blunt, the high arch formed by the gape being noteworthy. The mandible is large, prominent, and protrudes somewhat in front of the snout. The hyoidean region is well developed, though the branchiostegals are indistinct. The abdomen (*abd*) is very prominent and large, and has a silvery iridescent sheen superiorly. A trace of the choroidal fissure persists beneath each eye. Numerous blackish pigment-corpuscles occur over the brain; but only an interrupted line extends along each side of the anterior half of the dorsal fin. The pectorals (*pf*) form large fan-shaped structures directed upward, and the ventrals (*vf*), which are blackish in hue, are of great size; but instead of arising considerably in front of the pectorals, as in the adult, they spring by a pale base only a very short distance in front of the pectorals. These long black fins are about one-third the length of the fish, and when first seen with the naked eye they resembled a pair of powerful black spines, for the protection of the tumid abdomen. Four of the rays, as in the American form, are largely developed. The body is of a general pale or slightly silvery hue in the preparation studied, and the stomach contained minute copepods. A somewhat silvery form, only 2 mm. longer (viz., 8 mm.), shows the dorsal and anal fins almost separated from the tail. The head is now better developed, and the delicate branchiostegals are very evident. The pigment over the brain is very dark, and a dotted band proceeds from this region backward for some distance on each side of the middle line. A group of pigment-specks also occurs laterally below the posterior part of the dorsal fin. From the elongation of the body, the ventrals do not seem to be so long. This example was procured on the 21st July at 22 fathoms, but the same stage has been seen at the surface. In young forms, apparently pertaining to *Motella mustela*, the dark ventrals show dull yellowish rays.

The next stage (Pl. XVIII. fig. 5) reaches a length of 10 mm., and the examples seemingly belong to the same species. A silvery hue predominates over the cheeks, abdomen, and partially on the posterior region of the trunk. Over the brain and along the dorso-lateral line the black pigment is more abundant, while a blackish spot occurs a short distance in front of the tail. The continuity of the dorsal (*df*) and caudal fin (*cf*) is less prominent though still present, and the tail is more elongated—tapering slightly towards the tip. The arch of the mouth is still high, though the forward growth of the premaxillary region renders it less conspicuous. The black coloration of the ventrals (*vf*) is confined to rather less than the distal half of each fin, and the length of these organs is proportionally shorter in relation to the body of the fish. The eyes are really larger;

but the abdomen is less tumid than in the last stage. Specimens slightly older than this are represented by Mr COUCH (*Brit. Fishes*, vol. iii. pl. cli. and p. 113) as THOMPSON'S midge, and were referred by the late Dr GRAY to the genus *Coryphæna*, probably from the remarkable development of the ventrals.

Specimens 2½ mm. longer than the last described, viz., 12·5 mm. in length, show a large increase in the amount of black pigment on the dorsum, where it now gives rise to a mottled appearance, extending over the sides and tail. Only a few corpuscles exist near the ventral line behind the abdomen. The pectorals have increased in size and strength, whereas the ventrals, though still of extraordinary dimensions, are now only about one-fourth the length of the body, and are tipped with deep black, while the remainder (⅘) of each fin is very pale in colour. The sides are silvery almost to the base of the tail. In many of the specimens a parasite like a young *Caligus* projected from the branchiostegal region. The youngest examples of *Motella* above described occurred in 32 fathoms water off the Isle of May, about 7 fathoms from the bottom, the others were obtained in the same region in 25 fathoms water and about the same distance from the bottom.

When *M. mustela* reaches 24 or 25 mm. in length, the general silvery hue is marked, only the dorsum of the head and body being brownish. The five barbels are distinct, and the tips of the ventral fins do not project behind the pectorals, though their bases have now advanced considerably in front of the former. The eye remains comparatively large. The specimens of this size were obtained by the surface-net in Lochmaddy.

At 29 or 30 mm. many of the adult characters have been assumed, the brownish-black pigment having spread over the upper lateral regions. The tips of the ventrals scarcely reach those of the pectorals, the three anterior rays being furnished with long sensitive tips. The abdomen and lower lateral regions are silvery.

The older *Motellæ* obtained are characterised, as Mr DAY observes,* by their very bright silvery sides and dark bluish-black dorsum. The black axillary pigment occurs in most of these, but it varies in intensity. They range from 26 to 40 mm. That which most nearly resembles *M. tricirrata* possesses a pair of very short barbels or papillæ in the premaxillary region, but sometimes one is indistinct, and they probably disappear during the subsequent stages. The ventrals extend about as far back as the tips of the pectorals, but their bases are considerably in front of the latter, the second ray being the longest of the three specially developed. All the black pigment has now disappeared. Contrasted with *M. mustela* of the same length, the eye is somewhat larger, and the space between them narrower, while the barbels are shorter. The first dorsal appears also to be somewhat shorter (from before backward). The free rays of this fin are characteristic in all the species.

Two examples from the surface of the sea, south-east of the Isle of May, present only a single median barbel on the upper lip. Both show axillary black pigment, and in other respects correspond with the foregoing, except that the median barbel on the

* *Op. cit.*, p. 312.

upper lip is longer, as also is the barbel on the mandible, while the snout is less prolonged, the latter character being indicated by Mr Day. These examples measured 27 and 38 mm. respectively, and corresponded with *Motella cimbria*.

Unknown Egg with Oil-Globule (F).—A small egg, measuring ·034 by ·035, with a single oil-globule, and in the earlier stages agreeing with *Motella*, was captured by the trawl-like tow-net on the bottom in the early part of May and for some time thereafter. As soon, however, as the pigment appeared in the embryos its distinction from the common species (*M. mustela*) was evident (Pl. V. fig. 4). The reticulated cellular appearance of the contained embyro and yolk was another marked feature.

After extrusion the larva (Pl. XVII. fig. 4) measured about $\frac{1}{10}$th of an inch, and was characterised by the presence of yellowish pigment along the marginal fin dorsally and ventrally, blackish chromatophores occurring amongst the rest. The tip of the tail, however, remains uncoloured. The general surface of the body, head, and yolk-sac is dotted with yellowish pigment, and a few black chromatophores are present on the yolk and oil-globule. No pigment appears in the eyes. The oil-globule is situated inferiorly distinctly behind the middle of the yolk-sac, but a considerable interval exists between it and the posterior border of the latter, thus distinguishing it at once from the egg of *Motella mustela*. Moreover, the entire surface of the larva is covered with a somewhat coarse reticulation of cells with nuclei, which do not occur in the centre of the cells, but at their margins. On the third day after hatching the mouth had not yet opened, and the only new feature was the more general distribution of the yellowish pigment.

This larva was kept until the yolk and oil-globule had wholly disappeared. The chief change was the more conspicuous nature of the yellow chromatophores along the margin of the dorsal fin. The head is of a deeper yellow from the pigment over the brain, and the body has many minute yellow chromatophores mingled with black. The pectorals are tipped with yellow, and have the streaked mesoblastic basal region. The eyes are greenish silvery. The mouth is widely open. At this stage it somewhat resembles a pleuronectid.

An unknown larval fish (E) procured in February, and elsewhere* described and figured, approaches the preceding group (Gadoids) in the large size of the silvery eyes, which abut close on the maxillary border. At 10 mm. the notochord is straight, and embryonic rays occur in the tail. A marginal fin occurs along the ventral edge of the abdomen, which has a small yellowish oil-globule beneath the liver in front. Five black chromatophores occur over the head.

Young Pleuronectidæ.

Hippoglossoides limandoides.—The long rough dab seems to spawn early in the season, for during the trawling expeditions ripe specimens occurred towards the end of March; and some seemed to have discharged all their ova on the 21st March. Com-

* "Pelagic Fauna," *Seventh Annual Report, Fishery Board for Scotland*, 1889, p. 263, pl. iii. figs. 5–7.

paratively small specimens are productive. Northern writers give the end of winter as the spawning period.

After the stage in which the young of this species and Pleuronectids generally resemble the larval condition of other fishes, they begin to exhibit an increasing depth of the body, disproportionate to their length. In the earlier stages, when about 4·5 mm. in length, this flattening and depth of the body are diagnostic. Towards the tail an abrupt narrowing occurs, and the slender embryonic tail proceeds therefrom as a tapering straight process bordered by the embryonic fin, which runs from the head dorsally all round to the anus. The rays are longest at the base of the slender caudal process. Another feature of moment is the ventral projection of the abdomen, for it extends much beyond the line of the body as a prominent swelling. As aids in diagnosing the mutilated young flounders of this stage are the proportionally larger eyes in the young round fishes, and the structure of the tail; the depression of the snout between the eyes is also a noteworthy feature. The eyes, it need scarcely be mentioned, are quite symmetrical, as in other fishes.

The most prominent feature in the next stage is the thrusting upward of the terminal caudal "whip" by the development of the hypural elements and the inferior true fin-rays. The ventral margin is also often finely dotted on each side with black pigment. The hypural cartilages so largely increase that they form a deep vertical boundary to the tail, the terminal (notochordal) process being bent upwards, and appearing, when viewed externally, as a slight filament. The depth of the body at the base of the tail has greatly increased. The left eye now shows a tendency to move forward and upward, and a slight twisting of the frontal region is discernible, so that the symmetry of the head is no longer perfect. Small lateral buds indicate the ventral fins.

The most advanced specimens measured about 13 mm., and when one was placed on its side a small part of the left eye was visible above the margin of the head. Moreover, that eye was slightly anterior to the right eye, and its axis was directed somewhat forward. On the right side four black pigment-spots were situated at the base of the interspinous bones, and the same number, besides specks on the body posteriorly, occurred along the ventral region. On the left side only two were visible along the dorsal line, and a few scattered specks along the ventral, as well as on the posterior part of the body. The general outline of the body strongly suggested that the species was no other than the long rough dab, but the mouth seemed to be similar to the common dab. This latter feature may, however, readily alter afterwards. The dorsal and anal fins are still joined to the caudal by a marginal membrane without rays. This form ranged from 5 mm. to about 13 mm., and was captured in the mid-water net at the end of August. Next year (1887), however, similar specimens were procured towards the end of July, and one reached 14 mm. in length. Their distance from the shore, and the depth of water, besides their structural features, gave grounds for connecting them with the species mentioned. The young of the common flounder at other stages appear to approach it very closely.

Pleuronectes limanda, L. (Dab).—The ripe forms at St Andrews have generally been procured in April and May, but there is no reason to suppose that, as in other marine fishes, they do not overlap these limits considerably. The diameter of the egg is ·033 inch, or about ·825 mm.

As an example we may take a series fertilised on April 30 (1885) at 2 P.M. In these ova the perivitelline space is very small. At 4 P.M. the blastodisc was formed at one pole, and the nuclear zone covered it. At 5.30 P.M. the disc was in the four-celled stage, each sphere with a nucleus. Scattered granules, moreover, occurred on the margin. The morula-stage was reached at 10 A.M. on the second day (1st May), and the granular periblastic zone surrounded the disc, the nuclei being two or three deep. At 12.30 the disc had increased in diameter, showing finer cells in the centre, and larger at the margin. The periblast was broader, and nuclei could be seen under the margin of the disc by tilting the ovum. The disc had still further extended at 3 P.M., and the cells resembled large irregular nuclei embedded in a narrow protoplasmic envelope. On the third day the blastoderm had reached the equator, and the embryonic shield was well defined. On the fifth day (4th May) the embryo is fully outlined, and KUPFFER'S vesicle appears. The cephalic region has increased, but the optic enlargements are not outlined. In certain aspects indications of metameres are observed anterior to KUPFFER'S vesicle.

On the morning of the sixth day KUPFFER'S vesicle had considerably diminished, and about sixteen metameres were indicated, and they extended almost to the head. At 12.30 KUPFFER'S vesicle had sunk into the tissues of the trunk. The metameres have a rounded dorsal outline. The notochord is distinct from KUPFFER'S vesicle almost to the pectoral region, and slightly indicated in front of the latter. The lenses of the eyes were faintly outlined at 1 P.M.

On the seventh day (6th May) about thirty protovertebræ are clearly outlined. The otocysts are small, but well defined, and the cavity is ovoid and limited. The lumen of the mesenteron extends almost to the otocysts, and posteriorly it expands considerably, becoming attenuated, however, before ending blindly. The neurula is cleft in the middle line, and rises anteriorly as two bold ridges. Yellow chromatophores (round) are scattered over the head dorsally, and extend almost to the caudal termination.

On the eighth day the eyes are boldly outlined, and the otocysts have expanded, the oval chamber having increased in length and breath. The lumen of the mesenteron anteriorly appears to be bifid, an arm passing towards each otocyst, but ceasing before reaching the eyes. The protoplasm (periblast) enveloping the yolk has formed many reticulations. At 12 noon the notchord shows lens-shaped cells or vacuoles—partially alternate in arrangment, while at 6 P.M. it is completely segmented by bold fissures. The yellow chromatophores are more distinct, and though irregularly distributed may roughly be described as forming a double lateral line on each side, viz., a dorsal and a ventral. The surface in the cephalic region is rough from papillæ on the dorsal and lateral regions. The pectorals are rudely outlined, and the heart appears as

a solid transverse column, showing, however, a core when viewed on end. Active movements occur, so that the tail is sometimes drawn from left to right.

On the ninth day the trunk has lengthened, and the tranverse chambers of the notochord are much longer, leaving narrow intervening bars of the original tissue. The otocysts are larger, and show two otoliths. The cavity of the mesenteron stretches from the otocysts to the anal region.

The heart pulsates faintly and irregularly at intervals on the tenth day (9th May). The notochord is broken up into large and somewhat angular compartments. The pigment-spots show further development.

By vigorous movements the embryos, measuring about $\frac{1}{20}$th of an inch in length,* emerged on the twelfth day; but it has to be stated that in other instances, somewhat later in the season, and when the temperature was higher, they issued (*e.g.*, on June 2) seven days after impregnation. They were carried about by the slightest surface-currents, gently descending head foremost and again ascending by the usual wriggling motion. The pigment-spots are very distinct, of a lemon-yellow colour as already described,† and are grouped in two lateral bands. The liver forms a pouch-like prominence on the anterior portion of the alimentary canal. On the second day the pigment had increased anteriorly, forming irregular blotches on the cephalic region. On the fourth day the pectorals are about twice as large as on emergence, and an anal tract is forming, while in many the upward flexure of the caudal region is marked. They are about $\frac{1}{40}$th of an inch longer, and swim in small groups at the margin of the vessel.

On the seventh and eighth days the chromatophores are finely stellate, and the eye has much black pigment. The larvæ are very active, though when descending they often assume the reversed position. The snout is rounded and prominent; an oral aperture has appeared, and the mandible slightly projects. The basal process of the pectorals is marked, and radial thickenings are formed on the fin. The anus is not yet open, and no circulation is visible though the heart beats actively. The hyoid is well developed, and four branchial bars are distinct.

On the tenth day after emergence the survivors swam actively when disturbed, using their large pectorals like flippers, but they often lay on the bottom. The dark pigment of the eyes presents a greenish iridescence. The increase of the pigment over the surface, the opening of the anus behind the scarcely visible yolk-sac, the great angular development of the mandible, and the membranous opercular covering, are the chief changes. The stomach shows tranverse folds, but posteriorly longitudinal rugæ pass to the anal region. A dorsal elevation covered with papillæ gives a peculiar outline to the head. The embryos survived only a few days longer. ‡

* Mr Cunningham (*op. cit.*, p. 100) gives the length of the newly hatched larva at 2·66 mm. He does not allude to the characteristic lemon-yellow coloration.

† Page 791.

‡ The stages intermediate between the foregoing and the succeeding are at present no doubt confused with those of the flounder and other forms, especially as when brought to the surface they are generally injured, or as yet have only been examined in spirit.

Specimens 28 mm. in length are occasionally thrown on the west sands. They are distinguished from the flounders by their larger eyes and more elongated outline, even when the lateral line is invisible. Others 1½ inch long occurred in the trawl on June 7, while somewhat smaller forms were found in the stomach of a gurnard on the 20th of April.

Pleuronectes cynoglossus, L. (Witch).—Another form characterised by its comparative thinness, narrowness of body, great breadth of the embryonic fin, and the conspicuous character of the dark olive pigment, was obtained abundantly. It is distinguished from the young of the long rough dab, by the translucency of the body even after immersion in spirit, and by the nature of the pigment, which is finely dotted along the ventral edge in the young dab, whereas in this form only a few (about five) large isolated patches, blackish in spirit-preparations, occur along the dorsal and ventral margins of the body (Pl. XVIII. fig. 7). The depth of the embryonic fin exceeds that of the body, and the abdomen is prominent; the urinary vesicle being very visible posteriorly. A little pigment also occurs on the surface of the abodmen, and the marginal fin is of a faint dull yellow in life. Both sides are similarly coloured. The caudal region is abruptly narrowed, and the notochord proceeds straight outward even when fish is 8 mm. in length. The lower caudal rays are, however, cartilaginous as well as those above; all the others are membranous. The otocysts are large and well developed. The head and abdomen, at this time, appear disproportionately large for a body so long and slender. By the development of the hypurals the usual changes are brought about in the tail, and when the fish is 12 mm. long and about 4·5 mm. broad (Pl. XVIII. fig. 8), the marginal fin is appreciably narrower, while the interspinous elements appear along the edge of the trunk, and inferiorly the body now slants from behind downward and forward, so as to embrace the gut. The ventral fins are not yet visible. Five pigment-patches occur along the dorsal line as before, besides some minute spots at the base of the tail. Inferiorly, on the right side, two touches are present on the abdominal edge, and one at the curve of the rectum superiorly; three others lie in front of the caudal pigment-spots. On the left side the abdominal patches are somewhat less distinct. A little black pigment also exists on the tip of the jaw, at the ventral edge of its angle and on the prominent area below the pectorals. The right eye is apparently a little in front of the left. The embryonic tail remains with its superior rays, while the inferior rays (forming the main part of the caudal fin) are well developed. Parasitic *Caligi* are frequently attached to the anterior region.

When 14 mm. in length (Pl. XVIII fig. 9), the greatest breadth of the fish, including fins, is about 7 mm. The left eye at this time appears, in profile, above the head, and is distinctly in advance of the right. The pigment-spots on the right and left sides are nearly the same, though those on the right, perhaps, are more distinct; four patches occur along the dorsal margin and three along the ventral margin of the body. The touches on the abdomen are present, but somewhat altered by the growth of the tissues, and so

with those on the ventral margin as well as the head. Pigment-specks persist at the base of the tail. The body is now proportionately broader.

In specimens 2 mm. or 3 mm. longer, similar features as regards pigment and other points occur, but the left eye is mounting over the head, and the ventrals appear as minute buds, while the marginal fins of the specimens are still infested by young *Caligi*.

These specimens were generally procured E. or S.E. of the Island of May, in water varying from 18 to 29 fathoms, the mid-water net being floated about 4 fathoms above the bottom.

The earlier stages of this species have been observed by Mr J. T. Cunningham,* who secured the ripe adults in June by the trawl near Cumbrae in the Clyde. His oldest larva, however, represents a considerably younger stage than our fig. 7, Pl. XVIII., the latter being about 8 mm. in length, whereas Mr Cunningham's earlier form (rather more than two days old) measured 5·9 mm. Moreover, instead of three dark patches, there are four on the tail. It is satisfactory to have a fairly complete series of this species, which, on the eastern shores, is generally characteristic of deep water. Mr Cunningham's ova hatched on the 6th day, but they were under abnormal circumstances as regards temperature.

Pleuronectes platessa, L.—The ova of the plaice (which measure ·065 to ·069 in.,† or 1·65 to 1·7 mm.) were brought by Captain Burn, late of the 11th Hussars, on the 21st of April, having been fertilised two days before. The zona radiata is minutely punctured, and it is often peculiarly wrinkled. On the 28th the embryo is clearly outlined, and is conspicuous by its bright canary-yellow spots (Pl. V. fig. 6). The spots do not extend quite to the tip of the tail, but leave a considerable terminal portion bare. In one specimen a vesicle (*kv*), similar to Kupffer's, appeared in the mid-abdominal region, and was thus considerably in front of the normal position. It possessed a distinct protoplasmic covering. Moreover, a smaller vesicle appeared on the surface of the protoplasm of the larger. The heart of the young plaice presents the same features as in other pelagic forms, and begins to beat on the 6th day, and at 7.30 P.M. on the 28th April it pulsated forty times per minute. Its long tubular region lies to the left side, goes forward and forms a loop, turning backward just as in larval round fishes. The great breadth of the marginal fin is noteworthy, and it is well seen in the egg. In several examples film-like bands or ridges stretch across obliquely from the head of the embryo into the rest of the blastodermic area. As the pigment develops in the eyes some are finely iridescent, with a reddish-golden lustre, but in a day or two the silvery sheen surrounds the pupil. The eggs are hatched in nine or ten days, and the larva is conspicuous amongst its congeners, the flat-fishes, by its great size (Pl. XVI. figs. 5, 5*a*). This does not imply that it is more readily observable, for the larvæ are difficult to discern in the water. When about a week old the canary-yellow colour seen so distinctly posteriorly is found to be due to rounded corpuscles, which by transmitted light appear to be brownish, and more or less opaque. The marginal fin of the larva is of great breadth, though in

* *Op. cit.*, p. 101, pls. iii., iv., and v.

† Mr Cunningham (*op. cit.*) gives 1·95 mm.

ordinary views the body appears to be almost linear. A peculiar feature is the presence of minute dark pigment-specks on the ventral lobe of the marginal fin, whereas into the dorsal lobe (*ef*) only one or two of the yellowish corpuscles pass from the line of the body. In this early stage the otoliths are remarkably small—much less, for instance, than in the fluke of the same age. The larva swims actively at the surface of the water, and is not easily noticed except by its large iridescent eyes, which now and then exhibit a golden sheen. Like some other young forms already described, it floats head downward in the water, besides frequently boring its snout into the sand at the bottom of the vessel. When at rest it lies upon its side at the bottom, and if the background be dark the yellowish pigment is conspicuous, especially in the caudal region. A perceptible increase in length took place within a few days after emergence. There is so little difficulty in hatching these ova, that this species could be multiplied in any suitable locality which it did not already inhabit. Mr Cunningham* describes the yellowish spots as being in three rows on the lateral region of the embryonic plaice.

In April large numbers of young pleuronectids at and near 12 mm. in length occur in St Andrews Bay. The eyes in these are generally asymmetrical, though in the smallest forms very slightly so. In the most advanced the left eye projects above the dorsal ridge, but is mainly used for vision on its own side. The blackish pigment-corpuscles are chiefly developed along the ventral margin of the body, though in some the sides posteriorly, and the posterior half of the dorsal margin, have a few specks. The terminal region of the notochord varies from a long dorsal filament to a mere trace beyond the hypural elements in the older examples.

The foregoing may represent both the young of the plaice and the common flounder, the earlier post-larval stages in spirit not yet having been clearly separated.

At the mouth of the Thames, young plaice $1\frac{1}{2}$ inch and upwards abound in the nets of the shrimpers in October, and similar forms are met with at a later period at the margin of the sandy beach at St Andrews. In June and July, at the latter place, the smaller forms range from $2\frac{1}{2}$ to $3\frac{1}{2}$ inches, and these are probably the young of the previous season. It is a noteworthy feature in connection with this and other species, that the larger forms are characteristic of the deeper water, while the smaller, from 11 inches downward, abound in sandy bays (inshore water). The mature fishes (*i.e.*, those with the reproductive organs fully developed), as formerly shown, are thus mostly beyond the three-mile limit.

Pleuronectes flesus, L.—No form is better adapted for studying the development of pelagic Teleostean ova than this, though, as one of us has elsewhere pointed out, specimens in confinement seldom deposit healthy ova.† The comparatively rapid development of the embryo (six to seven days) is further favourable for a connected series of observations. The lateness of the spawning period in 1886 was also fitted to

* *Op. cit.*, p. 99.

† *Vide* account of appearance of retained ova, *Third Annual Report of Scottish Fishery Board*, 1885, p. 62.

bring out this feature, since the temperature was thus proportionally high. Moreover, as indicated in the *Report of the Royal Commission on Trawling* just mentioned, with reference to *Hippoglossoides limandoides* (Rough Dab) and other species, comparatively small specimens of both sexes are capable of successful reproduction. Thus females not more than $4\frac{1}{2}$ inches long, and males a little larger ($7\frac{1}{2}$ inches), have been paired with perfect success.

Ova fertilised at 4 P.M. on 1st April 1886, showed a wrinkled condition of the zona radiata after extrusion, but soon became smooth in outline, and the germinal cap or blastodisc began to be formed. In some, however, no such protoplasmic cap appeared for an hour or more. The two-celled stage was reached at 6 P.M., and the sixteen-celled stage at 9.45 P.M. The minute granules of the periblast were very evident in a profile view. In these ova the micropyle was generally found near the disc. Next morning (9 A.M. April 6) the blastoderm had made great progress, and the cells were nearly of equal size. At 1 P.M. it had extended almost as far as the equator. At 9 P.M. a large germinal cavity had appeared. On focussing down to the animal pole (the egg floating with the disc downward in the usual manner), a peculiar group of cells was visible, probably at the apex of the blastodermic cap, since the ordinary cells of the germ lay above them. Moreover, the two ova specially under examination presented certain (BROWNIAN?) movements of the granules of the region, as if from decay, yet such could not have been the case, as subsequent progress proved. On the 7th, at 9 A.M., the embryo appeared in the centre of the embryonic shield, as a long curved cylinder with an expanded and thickened head. It is proportionally longer than in round fishes, such as *Gadus morrhua*, *G. æglefinus*, and others. The cells of the blastoderm assume a honey-comb-like appearance—more distinct than in many Teleosteans. On the evening of the same day (the 7th) the optic vesicles are well developed, and the tail shows a more evident enlargement in front of the tip than in *Gadus æglefinus*. KUPFFER'S vesicle is present, while in many examples four or five smaller vesicles exist on the ventral surface of the caudal enlargement. On the 8th April, the vesicle referred to is larger, and situated just within the blunt knob of the tail. It is a large clear bubble-like vesicle, bounded by slightly granular protoplasm (periblast) of variable thickness. The yellowish pigment, characteristic of this species, now appears in the form of rounded corpuscles (Pl. XIX. fig. 5), which do not as yet send out radial processes. Occasionally one or two clear vesicles occur under the head, and they have the same appearance as KUPFFER'S structures. No other organs, except muscle-plates and neurochord, are visible in the trunk. On issuing from the egg the larvæ (Pl. XIX. fig. 5) float on the surface if lively, but if feeble they rest on the bottom in still water, *i.e.*, in the tanks, though it is probable that this latter phenomenon does not occur in nature. They shoot with a wriggling motion along the surface, and are recognised by the beautiful yellow grains of pigment; they appear, in fact, like minute clubs of transparent tissue with chrome-yellow spots. One evident patch of colour lies above the posterior end of the yolk, and another midway between that point and

the tip of the tail. The pigment is also scattered along the sides of the head somewhat symmetrically, and produces a characteristic appearance.

The mandible, about the eleventh day, has the form of a remarkable process in front. The larva differs from AGASSIZ's figure of *Pleuronectes americanus*, and shows much more pigment. The anus is open or nearly so. Instead of the hollow urinary vesicle behind the rectum a merely granular band passes downward parallel to the anal tract.

After the yolk has been absorbed, the little flounder presents a somewhat deeper aspect from increase of the marginal fin, as well as the more prominent pigment on it. Eight touches of black pigment occur at the margin of the dorsal fin and four behind the vent inferiorly. The large yellowish pigment-corpuscles (about eight in number) are confined to the body, only a series of minute ones being distributed on the marginal fin, a single speck generally existing in the centre of each blackish area. The latter are larger ventrally than dorsally. The trunk and intestine are minutely flecked with black points. The anterior region of the abdomen has a few yellowish specks. Ventrally about three yellowish touches occur along the edge of the muscle-plates. The eyes are bluish silvery. A dark mass of pigment lies internally at the pectorals, probably in connection with the segmental ducts. The anus is at the margin of the fin. Corpuscles occur in the heart. The mouth is widely open, and slight movements of the mandible take place.

As already mentioned, the ova of this species are very hardy, and the larvæ after emergence will live for some days in a very small quantity of water, even if unchanged.*

After the foregoing stages are passed, the little flounders are still pelagic, swimming about with eyes on both sides of the head. Like other flat fishes, however, as they get older they seek the lower parts of the water, though the eyes are still lateral and symmetrical. They are obtained by aid of the mid-water net at various stages in April, viz., some with the left eye still on its own side, though advanced a little and more prominent; others show the eye on the edge in front of the dorsal; while in a third series the left eye has gained the right side.

In April very transparent flounders, about 12 to 14 mm. in length, occur freely in St Andrews Bay, and also in the sandy pools amongst the rocks. A few weeks later (May 24) many occur at the mouth of the lade, which pours a fresh-water stream into the harbour, and are caught while swimming at the surface in company with *Mysis vulgaris*, young eels, and sticklebacks. These specimens had the eye at the edge, just as in the case of many caught in the sandy rock-pools. Moreover, each of the examples referred to had a parasitic *Anceus Edwardi* attached externally, generally near the margin of the muscle-plates at the base of the dorsal fin. When the crustacean was removed a deep pit in the tissues of the flounder showed the point of attachment. Further the *Anceus* immediately sought a new place, and began to pierce a fresh portion of the skin with its sharp spine-like gnathites, and tenaciously held to the fish. After boring a little, a tongue-like process was thrust out, apparently for suction. The irrita-

* *Vide* remarks in Report of Roy. Commiss. on Trawling, 1885, p. 363.

tion thus produced caused the flounder to dart about with great energy.* Young flounders, colourless, and of glassy transparency, rapidly develop pigment in the laboratory.

The remarkable appearance of the tail (opisthure, RYDER), with its marginal fringe of rays before any change takes place in the position of the eyes, recalls the condition of the tail in such extinct forms as KINER'S *Graphiurus callopterus*, in which, however, the vertebral column is prolonged in a straight line, instead of being bent up, and the ordinary caudal rays pass dorsally and ventrally from it. KINER'S form referred to, came from the bituminous shale of Raibl in Kärmarthen.†

The young flounders proceed a considerable distance up the fresh-water stream at a stage somewhat older than the foregoing.

If the forms observed in the muddy sand of the tidal pools, and also caught in the mid-water net in the bay in April, are the young of the season, their growth is remarkably rapid, even granting a much earlier period for spawning than has been observed at St Andrews (April).

During April, May, and June, very small specimens of the flounder occur at St Andrews in the shallow rock-pools, containing stunted Algæ (*Ceramium* and other forms), with a slight coating of grey mud. From their translucency the young fishes are invisible, especially on the greyish silt, in which they are often partially immersed, and, as ALEX. AGASSIZ noticed, the two prominent eyes alone attract attention, while the bodies of the fishes themselves cannot be seen. They are elongated and slender, about 12 mm. long and 5·5 mm. in total breadth at the widest part. At this stage the true pleuronectid features have been assumed. They swim with the dorso-ventral line horizontal (the right side uppermost), and dart about with rapidity, frequently in confinement leaping over the margin of the vessel. They are fond of attaching themselves to the perpendicular sides of a glass vessel, as if their left (white) side had a sucker, but the adhesion is simply due to the muscular action of the whole surface. Both eyes are visible from the right side, though the left eye is more or less lateral in position, or capable of looking slightly downward. In company with them, plaice of the same length occur, being distinguishable as broader and thinner fish, with the left eye not so far to the right, and the ventrals as mere rudiments, while those of the flounder are well formed.

The flounder is apparently a considerably older fish, and its left side is quite white, while in the plaice the pigments formerly mentioned occur. The coloration of the flounder varies rapidly, and though, when first captured, their anatomy is readily observed from their great translucency, yet, as indicated, a few days' exposure to an increased amount of light, from absence of shelter in the tanks of the laboratory, causes such a development of pigment, that they are useless as transparent objects. The blackish pigment-spots persisting after preservation, present a close approach to those in the young plaice of the same size. Thus along the dorsal body-line five pigment-spots occur, and four along the ventral line, almost the same number as in the former species. The general

* The food of these flounders consists of young *Gammari* and similar Crustaceans.

† *Sitzungsbr. der K. Akad. Wien. Naturwiss.*, Bd. 53 and 54, 1866, p. 155, Taf. i. fig. 1.

surface of the body is, however, much more generally studded with pigment-patches and cells, and the touches on the marginal fin are better developed. On the other hand, except a few minute grains along the body-line, the whole left side in some is white. The black pigment-spots in the American flounders, figured so deftly by ALEXANDER AGASSIZ, show similar features, and the spots described are very generally distributed.

The difficulties in diagnosing from size alone, are well illustrated in this species. Young forms, captured at different times, measured 9 mm. on the 15th April, 9 to 27 mm. on the 26th April, 15 mm. on the 24th May, 8 to 30 mm. on the 8th June, 10 to 18 mm. on the 18th June, 80 mm. on the 27th June, as well as 40 and 94 mm., while many ranged on each side of three-quarters of an inch. In July from 22 to 32 mm. In August, many captured in sand-pools near the estuary of the Eden were only 12 mm.

Rhombus maximus, Will.—The ripe ova of the turbot were procured from a female of 12 lbs., on the 10th July, during the trawling expeditions of 1884.* They are very small, only a little larger than those of the rockling, and the embryos, many of which were hatched from pelagic ova of the same appearance, captured by the tow-net on the spot, are likewise small. This seems to have been the first occasion on which ripe eggs of this species had been procured in this country. No oil-globule is present.

A post-larval form procured in August in considerable numbers, both south-east of the Isle of May and off the Isle of May rocks, is apparently the turbot. The youngest example, the eyes of which are still symmetrical, measures about 6 mm., with a maximum breadth of about 3 mm.† The larval tail projects backward and slightly upward, and is still surrounded by the embryonic fin. It protrudes considerably beyond the inferior fin-rays developed beneath it. The head of the fish is proportionally large,—larger, as compared with the length of the fish, than in any other form examined. The mouth is large. The dorsal line is nearly straight from above the otocysts to the base of the tail, but the ventral line slopes rapidly downward from the tail to the anus, and again rises with an anterior curve to the jaw. Thus the body has a triangular outline. The dorsal and anal fins have rays, and are of moderate length. Papillæ indicate the rudiments of the ventral fins. Both surfaces of the body are minutely speckled with black points, but the right is more uniformly marked in this way. The specks extend to the marginal fins, but not over them.

The changes which follow—as seen in the next older forms—are the slight increase in depth and roundness of the body posteriorly, the elongation of the rays of the marginal fin, and the appearance of five or six touches, caused by aggregations of dots, in the dorsal, the ventral still remaining speckled as before. The closely approximated ventral fins have likewise minute black points, but the pectorals remain pale.‡ The right eye meanwhile is gradually passing upward, and the embryonic fin is rapidly disappearing.

* *Vide Report*, p. 363.

† The spawning period of the turbot in the Baltic is given as May and June, but in the North Sea, July (MÖBIUS and HEINCKE).

‡ A larval pelagic flounder of Mediterranean (*Peloria rüppelii*, Cocco) has remarkably pedunculate pectorals, a feature present in many young fishes (EMERY, *Reale Accad. dei Lincei, Classe di scienze fisiche, math*, &c., xiv., 1883).

The next phase consists in the strengthening of the abdominal wall ventrally, the increase in the distribution of the pigment, the left side still remaining slightly speckled, while the right is densely coloured; the more distinct grouping of the pigment in "touches" in the fins both dorsally and ventrally, and in the progress of the right eye towards the left. The marked notch behind the angle of the mandible, and the elevation of the head behind the right eye, are also noteworthy features. When the right eye mounts on the dorsum, the dorsal fin forms a high arch over it, and the body has considerably increased in depth in comparison with its length. A specimen about 9 mm. in total length has a depth of 6 mm. Besides the "touches" of pigment on the fins, a few minute blacks points are scattered over the left surface—the right being covered with minute dots almost as densely as before.

A subsequent stage to the foregoing is shown in Pl. XIX. fig. 1, but no specimen in our collection affords the intermediate or transition-features so as to ensure certainty by continuity of stages. The occurrence of the pigment-touches in the dorsal and anal fins, however, and their character, the general shape of the body, and the appearance of the head, support the probability that they are stages of the same species. None show traces of the spines, although the right eye has now reached the edge of the face. The eyes appear to be larger. Though some examples are no longer, they are somewhat better developed, a feature common in such fishes, certain individuals often reaching an advanced stage more rapidly than others which are even larger. In such an example as figured in Pl. XIX. fig. 1, which was 9·8 mm. in total length and 7 mm. in total breadth, the tail measures 2·5 mm., so that the length from the snout to the base of the tail is nearly equal to the total breadth. The right or ventral surface is pale, with the exception of a few irregular black specks and streaks, while the dorsum is streaked across with black pigment-bands, which have a remarkably regular arrangement, the touches in both dorsal and ventral fins being joined by intermediate streaks, the head and abdomen only showing scattered points. The under surface is quite pale, and thus contrasts with the minutely speckled right surface of the specimen in the earlier stage. The dorsal and anal fins have long rays toward their posterior border, and the body of the fish acquires a somewhat quadrate form. The ventrals still show the pigment-streaks, and thus are in uniformity with the anal in a lateral view. Moreover, a characteristic larval cuticular spine appears at the posterior part of the head, above the opercular margin, and somewhat in front of a vertical line running up from the pectoral, while a smaller spine projects a short distance beneath. Both right and left spines are well marked in another example a few mm. longer, and which shows a similar coloration. They are probably protective spines, since they disappear as the fishes grow older. Their appearance on both sides, after the right eye is at the edge, indicates the possibility that, for some time, the fish may occasionally resume the vertical position in swimming. Further, the presence of a young *Caligus* fixed to the right side supports this view. A specimen, 20 mm. long, captured at the surface, shows the right eye just on the ridge, with the dorsal fin close to its posterior border.

When the turbot reaches a total length of 21 mm., and when the left side has assumed the characteristic mottling of the adult, the spines above mentioned have disappeared from both sides, and the right shows minute black pigment-specks. The right eye is now on the left side, and the dorsal fin has advanced in front of it. The pectorals have considerably diminished, but the ventrals retain their proportional size. Specimens of these dimensions appear to be nearly a year old, and such are frequently found swimming at the margin of the sea.

Our knowledge of the development of this species is meagre and very unsatisfactory. Thus Buckland says that the turbot spawns in early summer, Parnell states in spring, and the young are seen in pools and on the surface in June and July. It is asserted in Day's recent work* that "the young turbot would appear to swim on its edge for a longer period than the generality of our flat fishes;" and it is added that a specimen an inch and a half in length (August) may be taken to be two months old. Day cites Mr Dunn to the effect that they are hatched in June or July. "For the first month they are quite black, and swim on edge like a 'John Doree.' Then their skin commences to mottle with white and brown, and their right eye begins to pass over to the left side of the head. Next they become white underneath, and of a light leaden colour on the upper surface, and during the period they remain of this shade on the back, which is until they have passed two months of age, they swim on the surface of the sea." Some of the turbot of the east coast (Scotland) at any rate spawn in July. A female on the 10th of that month, as already indicated, contained many ripe ova, which were of comparatively small size and floated buoyantly in sea-water.† Unfortunately no male could be procured on the occasion in question; but many ova of precisely the same size and appearance were obtained on this ground in the tow-net and hatched, the larval fishes resembling in all the usual points those of other Pleuronectidæ. They are very small larval fishes on emerging, and experience has shown that they could scarcely have the size and appearance mentioned by Day in two months.

So far as present knowledge carries us, the young turbot of the season, hitherto procured at St Andrews, measure about 11 mm.‡ at the end of August. Others, again, captured in the estuary of the Eden on the 25th July, had reached 23 mm.; and one, from the surface, on the 20th August, 29 mm., some blackish pigment still remaining on the right side. In April, again, specimens about 6 inches in length occasionally occur in the salmon stake-nets. If these stages refer to a year's growth, the latter would seem to be slow, yet only very great irregularity in regard to the spawning period would explain such differences.

Rhombus laevis (Brill).—No ripe brill has hitherto been seen at St Andrews, and none occurred during the trawling expeditions in 1884. Raffaele considers that a pelagic ovum, with a large oil-globule, which he procured in February and March in the Bay of Naples, pertains to this species, and he is probably right. A similar ovum with a pale oil-globule

* *British Fishes.*

† *Report of H.M. Trawling Commissioners*, 1884, p. 263.

‡ Total length.

(which thus differs from that of the gurnard) has occurred in St Andrews Bay several times in February and March. The oil-globule did not appear to be proportionally large, and lay in the yolk under the lateral expansion of the embryo. The pigment in the latter was well developed, and mainly yellowish, though black chromatophores were also present; the eyes were silvery iridescent in the most advanced forms. From the resemblance of the contained embryo to the plaice it was at the time supposed to be that of the brill, and subsequent consideration of the remarks of other observers have strengthened this view.

A specimen, apparently of the brill, though resembling the megrim, about 12 mm. in length, with a breadth of about 6 mm., was procured on August 31, 1886, off the Isle of May. The dorsal fin has about six dark bands at intervals, and the anal, which was much injured, seems to have had similar touches. The right (ventral) surface, again, instead of being white, is everywhere minutely dotted with black points. On comparing with a turbot (*Rhombus maximus*) of the same size, the body is seen to be narrower, the eyes larger, and the pectoral fins somewhat larger, while the comparative absence of pigment from the dorsum, and its presence, as minute dots, on the ventral (right) side are also diagnostic. In the former the head has less of the angular form of the turbot, this difference being mainly caused by the roundness of the angle of the mandible, and the smallness of the mouth. The specimen certainly resembles *Arnoglossus;* but the last-named feature, the smallness of the mouth, is a point of dissimilarity.

The subsequent stages of the brill have not yet been fully investigated, and they are not often met with in St Andrews Bay, not hitherto, indeed, till they reach 10 to 11 inches, when they are common in the local trawls in September.*

Solea vulgaris, Quensel.—On the 1st August 1884, a sole was captured 10 miles from land (off St Abb's Head), with ripe ova, which floated buoyantly.† No male was obtained, so that the development could not be followed. Mr Cunningham‡ gives March, April, and May as the spawning period of the sole, but he had overlooked this observation. Off the eastern shores of Scotland, therefore, the period extends from May to August.

In the mid-water net on the 6th July a few eggs appeared for the first time along with some of the gurnard, and they have since been more plentifully obtained by the trawl-like tow-net on the bottom towards the middle or latter end of May. Like other pelagic ova they are translucent, but they have the peculiarity of a more or less complete ring of minute oil-globules in groups, of a yellowish-white colour from refraction of the light, for when viewed by transmitted light they are faintly straw-coloured. When floating, the ring of oil-globules is superior as in other instances, the disc being inferior. Besides the ring mentioned, a few small groups occur here and there at other parts. Under a lens the egg indeed appeared to be flecked with yellowish-white pigment. In

* *Vide Trawling Report*, pp. 358 and 361.

† *Report of the Trawling Commissioners*, p. 363.

‡ *Jour. Mar. Biol. Assoc.*, N.S. i. p. 18, where an excellent account, with figures, of the early stages is given.

diameter the ovum measures ·045 inch. The large oil-globules have a diameter of ·0015 inch, while the smaller measure ·0004 inch in diameter. The capsule, in a few slightly undulated, is somewhat thick and tough, so that considerable force is necessary to rupture it. The zona is very distinctly punctate, even more so than in that of the plaice (Pl. I. fig. 20). In one example the surface of the zona was covered with flattened papillæ, giving it a scabrous aspect (Pl. X. fig. 7). In the early condition of the blastoderm the border of the yolk under it presented a few large vesicles (Pl. XXII. fig. 1), which projected beyond the edge of the periblast, and at a later stage this vesicular condition extended round the greater part of the yolk, except just at the tail of the embryo. Moreover, pigment rapidly develops over the surface of the yolk as well as on the head of the embryo, and it has a dull whitish or faintly yellowish hue, in marked contrast to the yellow tint of the gurnard.

When the embryo is fairly formed (Pl. II. fig. 11), the groups of oil-globules change their position, most occurring along the ventral surface of the embryo, as in the egg of a *Solea* (?) described by Raffaele (No. 125*a*, p. 42, Taf. 1, figs. 33 and 34).*

The oil-globules in this egg comport themselves differently from the single globule in other eggs, *e.g.*, of the gurnard. They do not move freely, so far as observed, at any period of development, but retain their positions during the motions of the ovum. Their relation to the periblast must therefore differ materially from that in the gurnard already described. Raffaele considers they are in the cortical protoplasm, which divides the vitelline segments, and move with the latter. They certainly advance with the rim, but their subsequent arrangement under the developing embryo is a remarkable feature, indicating, indeed, the probability that something like a streaming of the protoplasm of the periblast takes place about the period of the closure of the blastopore, so as to carry the globules under the developing embryo.

While in the living egg the foregoing is the condition so far as can be observed, it is otherwise in the dead egg after the lapse of a day or two. In a dead egg at the morula-stage, the oil-globules (now somewhat larger and of a dull yellowish colour) had grouped themselves at the upper pole, the disc being at the lower. When the disc was placed uppermost the oil-globules moved up to it at first apparently on the surface of the yolk, but a more minute examination showed that they also moved through the yolk. It is clear, therefore, that a change had occurred in the protoplasmic investment of the yolk so as to release the oil-globules, which to some extent had coalesced, and permit them to pass through it.

The eggs develop with moderate rapidity, so that those with the rim about a third over, and which presented segments in the periblast under the blastoderm (forming the vesicular condition), hatched on the fourth day thereafter. The larval sole is a characteristic form (Pl. XVII. fig. 13), the entire body, yolk-sac, and marginal fin being minutely

* Mr Cunningham, in his recent paper, describes the oil-globules as aggregated on each side of the embryo, though there are a few groups at other parts of the surface of the yolk. He figures other stages than those given in this paper, and shows the vesicular condition at a different period from that in our fig. I, Pl. XXII.

speckled with opaque yellowish-white pigment. This pigment is arranged in interrupted touches on the body and marginal fin (dorsal and ventral), behind the yolk-sac, so that the pleuronectid character is early indicated. Moreover, the presence of pigment at the extreme margin of the fin, both dorsally and ventrally, gives great apparent depth to the body of the fish. The yolk-sac is comparatively large and globular, sustaining the larval fish readily in the water, either as in ordinary cases (sac uppermost), or suspended from it tail downward. Occasionally it remains in a vertical position with the head downward. The large and rounded condition of the yolk-sac causes the active little fish to roll over during progression, so that it often advances in a screw-like fashion. While in lateral view the yolk-sac is somewhat ovoid, it is quite circular when seen either from the front or the rear (Pl. XXIII. fig. 10). The same condition probably causes the larva to make frequent gyrations. It would appear to be one of the most restless of the group, seldom remaining quiescent under examination more than a few seconds. It is not quite 3 mm. in length. The oil-globules form two main groups, one series running from the heart obliquely backward to the region of the pectoral fin, the other at the posterior part of the yolk, and extending ventrally along the posterior border (see fig. 13, Pl. XVII.). They slightly vary in different specimens. One or two isolated groups also occasionally occur along the ventral border. All retain their periblastic position. No pigment other than the superficial chromatophores exists in the eyes.

The vesicular condition of the yolk is not readily seen after hatching, though it can be made out by manipulation of the light, or in favourable positions. The vesicles appear to be flattened out at the margin of the yolk. In a specimen of the first day, peculiar vesicles, having a faintly pinkish hue like those of the blastodisc of the haddock, were visible on looking down on the yolk-sac of the larval fish floating head downward (Pl. XXIII. fig. 10). They were grouped in the neighbourhood of the posterior oil-globules, and occurred nowhere else in the yolk. They differed in appearance from the ordinary vesicles at the border of the yolk, and resembled peculiarly modified protoplasm. Their globular condition was distinctly visible during the motions of the larva, and they were situated in the transparent yolk within the oil-globules. One of the vesicles presented a series of minute granules in its interior. They were observed subsequently in various specimens.

One example presented a vesicular process over the brain, so that it had a hooded aspect, but this enlargement appeared to be abnormal.

On the second day the yolk has considerably diminished, and the posterior border carries the groups of oil-globules forward with it, leaving a larger space between it and the vent, while the pericardial chamber has become distinct in front. Minute pigment-specks now appear in the eyes. The peripheral segments of the yolk are still indicated.

On the fourth day the yolk has still further shrunk. The cavity of the mouth is formed, though no external aperture yet exists. The vent has not yet opened, indeed the gut terminates a little within the margin of the fin. The clear vesicles observed in the yolk of the former specimen were still visible, and one had a minute globule of oil in it.

A feature of interest in several was the remarkable size of the optic lobes, which projected dorsally so as to give the head a "hooded" aspect, as in the condition before mentioned. The agility of the little larva is characteristic.

Three days later the activity of the larval fish had become even more marked, and it seemed in a state of perpetual movement, the only interval being for a second or two after a long course through the vessel. This almost ceaseless movement is probably connected with respiration, the now widely open mouth being driven against the water which thus rushes into it. The pectorals vibrate like those of *Hippocampus* (a resemblance the more appropriate from the dermal process on the vertex), and the tail appears to move as rapidly. The larval soles chiefly kept the bottom of the vessel at this stage, swimming obliquely with the head directed downward, as if boring into the bottom or sides. Occasionally, however, a swift dart was made right across the vessel, or a shorter one as if capturing prey. The mandible moves rapidly as in respiration. The yolk has now diminished to a small mass anteriorly—with the groups of oil-globules crowded together, while the posterior region of the abdomen is occupied by the viscera. This forward progress of the yolk is interesting, for while different conditions occur in different groups, one of the most common is the absorption of the anterior region, and the consequent presence of the diminished yolk posteriorly. Another feature of note is the occurrence of a prominent fold along the ventral margin of the abdomen. The pigment seems in some to be more ochreous, and to have less of the dull yellowish-white (like Tripoli powder) so characteristic of the early condition. Along the dorsal margin of the muscle-plates are a series of pigment-patches, which appear to be more numerous than in the example of the post-larval stage elsewhere described,* but variations may occur in this respect.

As the larval sole gets a little older, for instance two days subsequent to the preceding stage, the pigment becomes more distinctly ochreous, and the yellow chromatophores along the dorsal edge of the muscle-plates show signs of increase. Moreover, the pigment-spot on the occiput so characteristic of the subsequent stage is outlined. Eight distinct pigment-patches occur behind the former, one of the posterior (seventh from the occipital) being larger and almost meeting that from the inferior edge. The character of the head is as peculiar as in the previous stage, and the eyes are directed more or less forward (forward and outward), so that the active little fish can readily see in front. The yolk has now shrunk to a small mass under the liver—in front of the gall-bladder, and is not easily distinguished. The change from the buff or stone-coloured, or even the dull yellowish-white, of the early stage, to the ochreous tint of the present one is a feature of interest. Moreover, one of the most marked changes is the disappearance of the yellowish-white pigment from the edge of the marginal fin, so conspicuous in the early larva, and which renders it so easily observed in a glass vessel. The speckled condition may be associated with the more helpless stage, when, perhaps, it frequently rests on the

* *Vide Ann. Nat. Hist.*, Dec. 1888, p. 469, and *Seventh Annual Report, Fishery Board for Scotland*, 1889, where a coloured figure is given.

bottom, but this is conjectural. At any rate, the border of the marginal fin, at this and the subsequent stage elsewhere figured, is so translucent as to be generally invisible, only the pigment-touches arising from the border of the muscle-plates being seen. The other parts of the head and body, as well as the ventral surface of the abdomen, are speckled with ochreous and black pigments. It would seem that the pale buff or yellowish-white pigment of the early larva is transitory, for by and by the ochre-yellow, beginning at first as very minute points over the head and body, gradually spreads and supersedes the yellowish-white, which disappears. The differentiation between the two is clearly seen at certain stages, the yellow being characteristic of the body, the pale buff or whitish of the marginal fin. The pectorals have their fan-like distal regions directed forward, so that the larva seems to row itself onward by their rapid motion. The basal parts of the pectorals are also invaded by the yellowish pigment. The eyes are silvery with black pupils, and a dark arch occurs superiorly. The great depth of the head and the prominent ridge over the optic lobes are characteristic. Moreover, the skin-fold along the median-line of the abdomen next day was marked by a central hiatus, so that it formed two portions. Further, the anterior one in a day or two became broad and almost vesicular.

Zeugopterus punctatus.—A female example distended with ova was obtained in a pool near the laboratory, on the 16th May. Most of the ova were unripe, but here and there a translucent egg (Pl. I. fig. 6) occurred, especially anteriorly. They had a diameter of ·042, that of the conspicuous oil-globule being ·008. Though, in all probability, not so large as perfectly mature eggs discharged into the sea, the size is approximative. As might be expected from the comparative scarcity of the adult off the eastern shores, the pelagic ova are extremely rare in tow-nets; indeed, so far as known, none have been met with.

A post-larval example, 9 mm. long., was captured by the mid-water net at 25 fathoms, south-east of the Island of May, 30th August 1886, though unfortunately it was considerably injured. It is easily distinguished from the turbot of the same size by the much larger bright silvery eyes, and by the outline of the body. The right eye is prominent on the edge and its axis is directed laterally. The abdomen appeared to be prominent. It is an older fish than the turbot of the same length.

The size and prominence of the eyes in the latter stage is noteworthy, for when the fish reaches the length of $3\frac{1}{2}$ inches they are proportionally less, and moreover they are deeply sunken.

Unknown Larval Pleuronectid? (A).—When using the tow-net on July 9, 1884, on a trawling expedition 47 miles east by south of the Island of May, and over very rich ground, a larval fish about 3 mm. was obtained by one of us. At first sight (after preservation) it resembled a heteropod, for a cylindrical process projected from the anterior end, and the position of the yolk-sac and other features increased the likeness. The anterior process, however, is a hernia cerebri, and it must be remembered that the optic lobes in the Pleuronectids are prominent. The mouth is indicated by a faint slit. The marginal fin is well marked, extending from the front of the head to the tail, then forward to the anus. Here it splits, a fold running along each side of the yolk-sac to the posterior part of the mandible.

No form hitherto examined shows this double frill so well, a feature probably connected with the peculiar condition of the ventral surface of the abdomen. In relation to the latter, we have immediately below the small and vertically elongated pectorals a spherical body, the liver, then a smaller mass (gut ?), and lastly the large ovoid swelling of the yolk, which is closely applied to the gut above and to the rectum behind. The latter is well marked, and appears to open by an anus at the tip.

Unfortunately the preservation of this specimen was defective and the sections unsatisfactory, but one feature of note was observable, viz., the fact that the yolk contained a large oil-globule surrounded by a belt of protoplasm in which were a series of small oil-globules, which thus formed a ring round the larger central one. The lateral fold on each side of the yolk showed epiblast outside a core of intruding mesoblast.

Certain features in this form approach those of the larval *Arnoglossi*, described by Dr Raffaele (125*a*, pp. 49–55). *Zeugopterus*, *Rhombus lævis*, and probably other Pleuronectids, however, also have an oil-globule in the egg.

Ovum of Pleuronectid (B)—with large perivitelline space.—This large ovum, frequently met with in the trawling expeditions of 1884, and every year since, is characterised by its large perivitelline space, in which the yolk with the early blastoderm floats freely like a globule. At a later stage (Pl. XIII. fig. 3) the yolk keeps the upper arch of the egg with the embryo curved beneath. The zona radiata is comparatively thin, and it is sometimes difficult to obtain a clear view of the minute punctures (Pl. X. fig. 8). It is, however, not devoid of toughness. The contained embryo shows chrome-yellow and blackish chromatophores, the former extending nearly to the tip of the notochord. The newly hatched larval fish has been figured and described elsewhere,* so that it is only necessary to mention the later stages. The larval fish during the absorption of the yolk often shows prominent processes projecting from the surface of the yolk into the anterior space. When the yolk has been absorbed the fish presents three distinct yellowish bars behind the vent (Pl. XVIII. fig. 2), another at the latter (vent), and a line along the dorsum of the intestine, besides various touches of the same on the head and elsewhere. Stellate black pigment-corpuscles occur along with the yellow, and in the early condition are present over the yolk. The eyes soon assume a silvery aspect. The larval fish is active and comparatively large, resembling in certain respects the plaice. It is probably a pleuronectid.

Mr Cunningham describes the same egg before hatching.† It is not uncommon both in St Andrews Bay and in the open sea beyond.

Unknown Ovum (C).—Besides the foregoing, a small undetermined ovum occurred in the mid-water net in April, and probably belongs to the same group (Pleuronectidæ). The contained embryo is comparatively large and fills up the capsule almost completely. The larva issuing from this egg is represented in fig. 1, Pl. XVIII., the dull brownish-yellow pigment being characteristic. Moreover, the mouth of the embryo is open at the period of hatching—as in the plaice.

* *Vide Seventh Annual Report, Fishery Board for Scotland*, 1889.

† *Op. cit.*, p. 105, pl. vii. fig. 2.

Clupea harengus, L., and remarks on Clupeoids.—The youngest stages (A) of the herring were those hatched in the laboratory, 6th March 1885, and they measured 7 mm.* They are distinguished by their elongation, by the situation of the anus, which lies behind the commencement of the posterior sixth of the body, by the vesicular yolk, and by the ovoid condition of the yolk-sac. The mouth is conspicuous in some, in others it is not visible, therefore it is probable that there is diversity in regard to the degree of development at the period of hatching, as indeed the variable length shows. The pectorals stand at a slight angle to the body. The marginal fin is dilated in the caudal region. These specimens seem to be larger than Dr MEYER'S Baltic herring, which were only from 5·2 to 5·3 mm. in length, and the same length is given by KUPFFER.

Considerable progress had been made on the second day (stage B), for good examples measure 8 mm., and the body is less filmy. The yolk-sac is elliptical rather than ovoid, with the marginal fin carried forward on its surface posteriorly. A slight opacity occurs above and below the tip of the notochord. An opaque internal process also appears some distance in front of the anus. The mouth is a mere fissure, for the mandible is not much developed. A faint black pigment-line runs along the ventral border from the yolk-sac to the anus.

The next stage (C) is represented by examples caught in the mid-water net at 4 fathoms off the East Rocks, 29th March 1887. These Clupeoids are now about 10 mm. in length. The general outline of the fish is still much elongated, the snout is blunt, the eyes large and prominent, with a silvery lustre and a black arch of pigment superiorly. The mandible projects considerably in front of the snout. The otocysts are so large and prominent that the body appears to come off abruptly from the anterior region. The pectoral fins are similar to those in the foregoing stage, but the marginal fin has disappeared from the body, and a small elevation occurs on the dorsum (noticed even in examples two days old), some distance in front of the anus. The caudal arises about midway between the anus and the tip of the notochord (which is quite straight). Its outline is spathulate, and there are many embryonic rays. The ventral pigment now forms a dotted line on each side, between the pectoral region and the anus, and some specks also appear on the ventral border of the notochordal region at the tip of the tail. The anus is at the commencement of the posterior sixth of the body.

This form is evidently considerably older than the second, as the advances in the head, the hyoidean, branchial, and mandibular regions show. The branchial arches project freely ventrally. It is probable that it is at least a week or two older, a period which would correspond with the deposition in March, and those captured appeared to be about the same age, and were in great abundance amongst Sagittæ, Medusæ, Zoeæ, exuviæ of *Balani* and other forms. MEYER observes that free herring at the age of a month are 17 to 18 mm. in length, so that the foregoing, according to this author, would be considerably less than a month old. It has to be borne in mind, however, that there is great variation in the growth of fishes.

* The form of these was much more elegant than the larval herring represented by Mr CUNNINGHAM, *Trans. Roy. Soc. Edin.*, vol. xxxiii. pl. i. fig. 3.

About a fortnight later, viz., on the 14th April, young Clupeoids (stage D) were procured off the Pier Rocks by the mid-water net at 4 fathoms, along with a few young sand-eels, which are distinguished in spirit by their greater opacity and the larger pigment-spots forming an interrupted ventral line, as well as by the more or less median position of the anus. They are now from 12 to 15 mm. in length, and show the interrupted line of black pigment-spots from the pectorals to the middle of the body, after which the spots are so closely approximated that they seem to form one line to the anus, which has a speck or two externally on each side. These pigment-touches are all elongated antero-posteriorly, those behind the middle being linear. A few specks also appear on the ventral part of the caudal, next the notochord, and sometimes above the latter in those most advanced. The somewhat thick notochord passes straight backward, and the general outline remains spathulate. The embryonic fin-rays are still present, but the ventral region of the tail shows considerable opacity from the development of the hypural elements. A delicate narrow marginal fin is continued forward from the tail to the vent, and from the front of the latter a thin border runs ventrally almost to the pectoral region. Dorsally in the region of the process formerly noticed (*i.e.*, above a vertical line in front of the anus), a permanent dorsal fin is developing, its posterior border being somewhat abruptly sloped, while its anterior runs into a thin marginal fin which proceeds some distance forward. The base of this fin is opaque. The upper jaw has increased in length, but the mandible is only slightly longer. The mouth forms a large transverse slit. The brain and spinal cord are clearly seen anteriorly, and the otocysts are still large. The branchiæ communicate freely with the water.

At this stage the fishes are probably not less than a month old.

On the 28th April (two weeks subsequently) most have reached the length of 16 mm. (stage E), and the depth of the body has notably increased. The dorsal fin is larger, and so is the caudal, while the ventral opacity in the latter is also greater. The ventral and caudal pigment is more distinct, and most specimens present a median streak of pigment in front of the pectorals. The opercular fold is now growing over the branchiæ, which do not yet show papillæ. Viewed from above, the snout is broadly spathulate; and the alimentary canal is generally empty. Four days later all the structural features just mentioned were better marked, and the notochord showed a tendency to bend upward at the tip, but there was no increase in length.

A notable enlargement was observed on the 16th May (stage F), the length being now 20 mm., and the depth in the median region of the body was much greater, the part immediately behind the pectorals having, however, a less depth than the succeeding, but it was thicker transversely, so that there was less abruptness between the head and the body. The pigment-touches along the ventral edge are much larger, still, however, preserving their elongated shape and disposition—that is, arranged as an anterior series of larger and a posterior of smaller specks terminating at the anus. The latter is situated at this stage about the commencement of the posterior seventh of the body. The snout retains its spathulate outline, the pectorals are large, and the dorsal shows

fin-rays; the position of the latter fin, moreover, is unaltered. Behind the anus the fine rays of the anal fin are visible for some distance. A marked thickening, forming a rounded boss anteriorly, now exists under the tip of the notochord, which is slightly bent up. True caudal rays occur from the latter thickened region to the tip of the notochord, the embryonic fin completing the margin dorsally and in front ventrally. The direction of the inner border of this hypural thickening is from above downward and forward, the pigment marking it externally. The tail is thus being pushed upward. This stage is probably between two and three months old.

The next stage (G) at present available is illustrated by a specimen procured on 1st July, and measuring 27–28 mm., or about $1\frac{1}{16}$ inch. This has now assumed most of the characters of the adult. Thus the head has become more elongated and compressed laterally, and the upward bend of the mandible is marked. The depth of the body has much increased, so that the fish appears to be shorter. The dorsal fin is shorter, and has an elaborate muscular ridge at its base. It stretches from a line over the tips of the ventrals to the first third of the anal. No part of it extends in front of the ventrals—that is, it does not reach their anterior ends. A row of black pigment-spots runs on each side of the dorsum backward to the dorsal edge of the caudal. The anal begins at the posterior fourth of the body, instead of the posterior sixth or seventh, as in the earlier stages, and such is therefore a distinctive feature. The pelvic fins arise from a point rather in front of the middle of the body, and thus their position differs from that in the adult. The pectorals are still proportionally large, with a fan-shaped basal region and expanded rays. The caudal is deeply bilobed. When viewed from the dorsum the head smoothly glides into the body—from the great increase in the thickness of the latter. The caudal is homocercal, the basal (or hypural) region having a double crescent, and the pigment has increased in this and the neighbouring part of the base.

This form may fairly be considered as representing at this period the direct continuation of the stages formerly mentioned, though perhaps it is an advanced one of the series.

The second series of the season commenced with two examples procured on the 30th August. They nearly correspond with stage D of date 14th April.

On the 24th September, again, three stages occur, viz., those corresponding to stage E in spring; secondly, one, though only measuring 14 mm. in length, showing a further stage of development than stage F of 16th May (and possibly a sprat), for the hypural elements form a nearly straight vertical edge posteriorly, and the tip of the notochord projects from the upper angle; and thirdly, one a millimetre or two shorter than stage F, but somewhat more advanced than the previous (stage 2) in regard to depth of body, firmness of muscle, size of dorsal fin, and especially in the condition of the caudal, which has a straight vertical edge, with the permanent dorsal rays developing over the tip of the notochord.

A considerable margin must thus be given in regard to the spawning period.

On the 1st of October, again, one corresponding nearly to stage 2 of 24th September

was procured, the posterior edge of the hypurals not being quite vertical; while the upward bend of the notochord is in the form of a gentle slope.

Various stages were obtained on the 11th October in the same haul of the net, the earliest being like those last mentioned (1st October). The most advanced (about 19 or 20 mm. in length) had well-marked dorsal and anal fins, vertical hypurals, and just a trace of a notochordal spike at the dorsal edge, and therefore intermediate between F and G (1st July).

These remarks would tend to indicate that, at least, two spawning periods, as already known in regard to ova, occur in the neighbourhood.

Some whitebait procured in the Thames in June measured from 38 to 40 mm., and presented most of the adult characters. These perhaps represent the young of a late autumnal brood, though, judging from those procured in St Andrews Bay in July, a close approach must be made by the winter broods, especially in the warmer southern waters. Meyer's statistics would further corroborate this view. Similar Clupeoids abound in St Andrews Bay in March, and these may fairly be held to be the young of the previous season. According to Meyer's statistics, such would be about 5 months old, but probably they were from the ova of August, a period of seven months.

The gradual change in the position of the anus, by the elongation of the region between it and the tail, is noteworthy, as also is the relative position of the fins in the young and in the adult. The latter, which has been called the migration of the dorsal forward, was pointed out clearly by Sundevall and various subsequent writers, and appears to be characteristic of the Clupeidæ. The recent remarks of F. Raffaele (No. 125*a*) on this subject are of much interest.

Clupea sprattus, L.—About the beginning of May numerous transparent ova having a delicately reticulated yolk and somewhat thin zona radiata occurred in the bottom trawl-like tow-net. They appear to be the same as Hensen first found in the Baltic, and Cunningham obtained in the Firth of Forth west of Inchkeith, and which are described and figured by him. Hensen truly indicates the pelagic egg of the sprat as having a thin and transparent zona; while the larval form, he states, is distinguished from that of the herring by a slight flexure of the intestine.* Many are not quite round, their long diameter being ·044 inch, and their short diameter ·039. The reticulations of the yolk (Pl. I. fig. 5) are very fine, and much less distinct than indicated by Mr Cunningham, the margins of the sphere in an ordinary view presenting a confused series of lines. These eggs occur in very considerable numbers, and are evidently those of an abundant species. They are easily recognised from ova which resemble them in size by their translucency and the colourless embryo. They develop very quickly, and the larva soon escapes as a translucent form about 3·6 mm. in length, and, as Mr Cunningham says, is at first devoid of pigment. It is a characteristic Clupeoid (Pl. II. fig. 13), with the anus situated posteriorly. The yolk has the same kind of reticulation as described above, and it is comparatively large. Well-marked sense-organs are present on the sides, the last pair

* *Funfter Bericht der Komission z. wiss. u. d. deutschen Meere*, 1887, p. 40.

(opposite the anus) being larger than the others. Five pairs occur behind the yolk-sac, while a sixth exists in front of its posterior border. These organs are not opposite each other, but the left is a little in advance of the right. The marginal fin is not deep, and extends a short distance on the yolk. Very fine cells are visible on its surface.

The young fishes are somewhat delicate in confinement, the oldest example reared in the laboratory being represented in Plate II. fig. 13*a*—about nine or ten days after hatching. The yolk-sac has now shrunk considerably, and the snout projects forward as a blunt process. The surface of the yolk-sac anteriorly in one example is minutely papillose, but this is probably an abnormality. The pectoral fin is well developed, and the eye is slightly silvery. The mere change of these young fishes from a deeper to a shallower vessel suffices to cause distress, with speedy opacity and death.

Ammodytes tobianus, L.—Young sand-eels were found during the Trawling Expeditions in great numbers about the middle of April,* and they are similarly met with annually in St Andrews Bay, generally at a depth of 4 fathoms.

The youngest form associated with the sand-eel was procured in the mid-water net on the 29th March, and measured 6 or 7 mm. in length. The body is slender and elongated, while the head is large and bluntly rounded in front. The mandible projects considerably beyond the premaxillary region when the mouth is widely open. The pigment of the eyes (in spirit) is black, and scarcely a trace of the silvery sheen is noticeable. The eyes closely abut on the front margin of the snout. The notochord passes straight backward in the centre of the tail, which has only the fine and symmetrically arranged embryonic fin-rays. The delicate marginal fin had been injured, and only a remnant existed in front dorsally. The pectorals are largely developed. The anus opens about the end of the middle third of the body. Black pigment-specks are distributed along the ventral surface, viz., a single line from the pectorals a short distance backward, then a double line (on each side of the gut) to the anus. Behind the latter a very closely dotted line extends to the base of the tail.

A large number of larval forms similar to the foregoing, though somewhat longer (9 to 11 mm.), abounded in St Andrews Bay about the beginning of April, but their identity is at present uncertain.

What appears to be the next older stage (between 8 and 9 mm.) was captured on the 14th April. The marginal fin (which occurs all round) shows no differentiation, but the increase of the hypural elements and the true fin-rays inferiorly cause a slight upward bend of the tip of the notochord. A single dotted line of pigment passes from the pectorals to the tip of the tail, and a series of large pigment-corpuscles exists on each side of the alimentary canal in the middle third. The eyes now show a slightly silvery sheen. The mandible is still prominent. Cartilaginous rays occur in those parts of the dorsal and anal fins behind the vent. The pectorals are very large, much larger proportionally

* Möbius and Heincke give the spawning season of *A. lanceolatus*, according to Bloch, in May, and mention that Malm found a female with enlarged ova in June. *A. tobianus*, again, is said to spawn in summer (*i.e.*, from May to August).

than in the adult, the basal region being massive and muscular, while the distal forms a broad fan-shaped fin still having embryonic rays. It would appear that the relative sizes of the basal and the distal regions of this fin vary according to the different stages of the young fishes, the basal being especially large in the early larval condition, and gradually diminishing as the older stages are reached. These form most efficient organs during the purely pelagic life of such fishes. The branchial arches show small rounded papillæ (representing the branchial lamellæ). The otocysts are large and prominent.

This form seems to vary considerably in length in the subsequent stages, thus, *e.g.*, on the 28th April, some, though further advanced in general structure, were shorter than in the earlier condition. The snout shows less of the previous disproportion—the premaxillary region having grown outward so as to project almost as much as the mandible. The tail forms a symmetrical fan-shaped organ, the base presenting a straight vertical line (hypural), while the upper edge is pointed, from the tip of the notochord. The marginal fin is prominent from the vent inferiorly, and somewhat in front of this dorsally, rising a little in each case in the middle, and diminishing toward the tail, which it joins. Permanent rays occur in both, the anterior and posterior ends, however, being devoid of them. The black pigment forms in front of the anus two lateral rows of large spots, and a median more continuous series as far as the anus; while behind the latter a row of smaller specks exists on each side of the median line. Just in front of the pectorals a black pigment-bar occurs on each side.

At 12 mm. in length (also in April) the body has considerably increased in depth, while the tail-fin is now more elongated, and presents a median notch. The fin-rays in the dorsal extend distinctly forward to a line running upward from the anus, and less clearly for some distance in front of this. In the anal fin the rays reach the anus. These fins are at this stage distinctly separated from the caudal, and the base of the latter has a double crescent at the edge of the hypurals. The oblique bars of pigment in front of the pectorals, and the black pigment-spots along the ventral line are well marked, especially in front of the anus. The anal has now a double row of minute black pigment-specks at its base, a feature apparently coincident with the development of the rays. The mandible slightly projects beyond the premaxillæ. On 28th April they ranged from 9 to 14 mm. in length. Like other food-fishes, this species is subject to the attacks of parasitic young *Caligi*.

The next stage in the collection was procured in the mid-water net on the 5th May 1887, at the depth of 4 fathoms on 6 fathom ground, and they reached from 17 to 18 mm. in length, though some were less. The shape and arrangement of the pigment-spots generally agree with those mentioned in the last stage. The tail still shows two hypural crescents—with a dotted line of pigment running from the dorsal to the ventral edge. The rays of the dorsal fin, though short, can be traced forward to a point midway between the anus and the pectorals. The eyes are still proportionally large, and the mandible projects in front of the premaxillæ. The branchiæ have simple papillæ, with at most traces of crenations at the sides, and the gill-rakers are developing. The same

stage was found on the 11th October 1886, so that either the spawning period is prolonged, or two spawning periods occur.

On the 7th May 1884, a form still further advanced was caught in the tow-net in Aberdeen Bay, its total length being 27 mm. This would therefore correspond in some respects with the progressive growth of the foregoing, though the irregularity in this respect of marine as of fresh-water forms renders great caution necessary. The dorsal fin has now nearly reached a vertical line from the tip of the pectorals, but not quite, and it shows short fin-rays anteriorly. From the vent backward both dorsal and ventral fins have long rays—much longer than in the previous stage. The hypural crescents are crossed by the caudal fin-rays. The snout has grown still further in front of the eyes, and the head more closely resembles that in the adult. The branchial processes now present well-marked papillæ, and the gill-rakers are longer than in the previous stage. The former come off nearly at right angles, but the rakers slant differently. A membranous marginal fin appears ventrally from the anus about a third along the abdomen, and less distinctly somewhat further forward.

While the larval forms occur in March, it is necessary to state that others much larger are captured by the mid-water net at the same time. Thus, on the 29th or 30th March, three were obtained—18, 22, and 25 mm. in length respectively—such being in all probability the young of the previous season. Day concludes that they spawn in the autumn and winter months. He found in *A. tobianus* the "milt and roe" advanced in August and September, while Thompson states they deposit spawn at the end of July, but in some places they do so during the winter. Couch, again, considers the end of December the most common period, so that Day is of opinion that they continue spawning in the sand through the last few months of the year.

Again, an example, 33 mm. in length, was caught in the mid-water net on the 10th July 1887. Finely ramose pigment-corpuscles now stud the dorsum for a short distance behind the pectorals to the base of the tail, and the head and opercular regions have also an increased number. The tip of the snout is likewise similarly pigmented. The fleshy base of the pectorals has become much less in proportion to the distal region, from the increase in the length of the fin-rays and the consequent alteration in the shape of the organ. The pectorals, indeed, seem to attain their maximum at this stage. The elongation of the snout and the prominence of the tip of the mandible are also features of note. In regard to the pigment of this and other stages, it may be observed that considerable differences exist, according to the condition of the corpuscles. When contracted they form mere points—leaving the dorsum comparatively pale, whereas in expansion they constitute finely ramose pigment-areas with a central black point.

At 45 mm. in length (August) the snout still further elongates, and the hollow in the turbinal region disappears. From the increase in length and bulk of the body the pectoral fins do not have the same proportional size as formerly. The other characters are those of the adult.

Unknown Larval Fish (D).—An unknown larval fish (Pl. VIII. fig. 1) was pro-

cured in April, with the anus about the centre of the body, and a small mass of yolk containing a considerable oil-globule towards the posterior part of the abdominal cavity. It is less elongate than a Clupeoid. The gut passed backward for a distance somewhat longer than that between the snout and the abdominal wall behind the yolk-sac, and terminated about the middle of the marginal fin. A line of black chromatophores ran along the abdominal wall ventrally, and another (subnotochordal) was continued over the gut. The notochord was unicolumnar. In certain structural features this approaches the larval form of *Labrax lupus*, as shown by Raffaele * in his valuable paper, but the form of the fish appears to be more slender and elongated.

Another unknown form (G), procured in March, is characterised by a similar position of the anus (about the middle of the body), and the presence of a large oil-globule towards the posterior part of the abdomen. No trace of yolk has been observed.† It is a slender and elongated larval fish, eel-like in outline, though the precise relationships are unknown. It occurs very regularly in March. The larval eel has not yet been described, and any suggestion on this head is conjectural.

Cottus.—The youngest post-larval stage of a *Cottus*, which may be the earlier condition of *Cottus scorpius*, was procured at 4 fathoms in the mid-water net 4 miles off the West Rocks, St Andrews, 28th April 1887. It measured barely 6 mm.; the marginal fin is continuous, though there are indications of a differentiation anteriorly (first dorsal) and ventrally (anal). Two small flattened ridges indicate the ventrals. The pectorals are large fan-shaped organs. A few black pigment-specks occur over the brain, and a large dark band passes from the region of the pectoral to the anus on each side. The preopercular spines are developing. The notochord has a comparatively slight bend upward; the hypural elements are in process of rapid development inferiorly, the region being distinct from the larval tail, which is still large, so that the organ is bifid.

The next stage of this species was captured on the 22nd July 1887, in the mid-water net, at 33 fathoms, about five miles off St Abb's Head (W. by S.), in an area of 37 fathoms. The length was 7·5 mm. In this condition the young forms agreed with the older stage in presenting a pair of large tubercles on the nape, while the so-called anterior tubercles were represented only by a spine. Similar elevations occur in other *Cotti*, and are especially visible in young specimens. The black pigment-bands slanting downward and backward at the side of the abdomen are less marked than in the older form. The tip of the notochord is larger and more prominent than in the latter.

In life this form had a nearly transparent body, with a series of black spots along the ventral margin from the anus to the tail. The cheeks and under surface of the snout were also dotted with black specks.

Cottus quadricornis.—Examples (Pl. XVII. fig. 11) of a somewhat older post-larval stage than in the preceding form occurred in Crail "Har'st" on 20th July 1887, on ground 15 fathoms deep, with the mid-water net at 13 fathoms, and subsequently in St

* No. 125*a*, p. 15, tab. iv.

† This form is described and figured in the *Seventh Annual Report of the Fishery Board for Scotland*, 1889.

Andrews Bay. They were at once recognised by the deep black abdominal patch of pigment. The head is greenish, while the body is comparatively pale. The eyes are bluish, with a remarkable black St Andrews cross radiating from the pupil, the long axis being placed horizontally. Its length is 8 mm. Besides the conspicuous streak of black pigment which slopes downward and backward to the ventral edge, but does not meet that of the opposite side, stellate pigment-corpuscles occur on the under surface of the abdomen, a touch at the anterior region of the branchiostegal rays on the same surface, and a row along the ventral edge of the body above the anal fin. One or two specks also are present on the cheeks, and a considerable number over the brain, the latter being bounded posteriorly by a curved line which joins a median black band in front of the dorsal fin.

The four tubercles on the head are prominent, the posterior pair being the larger. The turbinal spines are not visible; but the four preopercular spines are well marked, the superior being especially distinct.

The first dorsal fin is only slightly arched, the second is continuous posteriorly with the larval tail-fin, which now lies at the upper angle, for the hypurals form a straight edge posteriorly. The permanent rays give a somewhat conical shape to the tail ventrally. The anal is likewise joined to the caudal; the pectorals form two fan-shaped organs, the rays passing close to the surface of the body—that is, the basal region is short, and thus in striking contrast to the organ in the larval Gadoids. The rays are massive though soft, and, as in the adult, present considerable free portions at the tip. The ventrals are small, and arise somewhat behind the bases of the pectorals.

The next stage in the development of this species is illustrated by a specimen 18 mm. long, procured in St Andrews Bay in the beginning of June. Traces of the St Andrews cross still occur in the eyes, the outer ends of the cross being most distinct. The head is of a dusky olive hue, with dull yellow over the brain, and the yellowish colour extends downward and backward to the upper abdominal region and in front of the pectorals, black chromatophores being studded on both regions. A dark belt passes from the first dorsal to the abdominal black band, where it ceases, then a pale bar intervenes between it and another broad belt occupying about two-thirds of the second dorsal (the anterior and posterior moieties being more or less free). A few blackish chromatophores occur dorsally, however, in the anterior moiety. No pigment is present in the tail beyond the latter region. The ventral portion of the abdomen is silvery; the pectorals have dark pigment at the base of the rays, but no further. The ventrals are small and pale. The two dorsal fins are distinct, and the first has a small touch of pale pigment anteriorly, and a larger posteriorly. A slight marginal fin connects the last with the tail. The head presents the two large dermal processes on the occiput, and a smaller over each eye. The three opercular spines are prominent.

Agonus cataphractus, L. (Post-Larval stage).—A peculiar form (Pl. XVIII. fig. 11) was procured in the mid-water net at 4 fathoms on ground 6 fathoms deep, St Andrews Bay, April 4, 1887, and is now identified as the young of the above species. It is remarkable for the great depth of both dorsal and ventral regions of the marginal fin, the outline

being thus somewhat spindle-shaped. The snout is comparatively blunt, and the large size of the eye gives a resemblance to the condition in the Gadidæ, and to some extent also to that in the Pleuronectidæ. The auditory capsule is large, a prominent elevation of the outline occurring in the region. The jaws present the proportions in the groups just mentioned. The action of the heart is readily seen through the large opercular aperture.

The body is elongate, about 7 mm. in length, the tapering extremity of the notochord being bounded by a somewhat lanceolate embryonic fin, in which the rays (embryonic) are developing next the base. The abdomen presents a marked incurvation in front of the rectum, and the anus is prominent. The pectorals are large and fan-shaped.

The pigment is mainly of two kinds, viz., grass-green and black. The head shows black pigment over the otocysts, black and green in front of the eye, and on the branchial and mandibular regions. From the posterior margin of the opercular aperture to the base of the pectoral the same pigments occur. The pectorals have regular rays of similar pigment—tinged with pale greenish. The abdomen is covered with black and green pigments. The dorsal and ventral edges of the body have a series of black pigment-corpuscles, the former extending from behind the pectoral to the last vertical bars of the dorsal marginal fin, as shown in the sketch; while the latter extend from the vent to the narrow part of the tail. When viewed from the ventral aspect, a broad bar of pigment stretches between the pectorals, and a considerable quantity is scattered over the abdomen. In a smaller specimen the opercular fold is rendered distinct by the black pigment in front of it, and the pale region behind it. The deep parts of both dorsal and ventral areas of the marginal fin have peculiar vertical streaks of greenish, and rows of black pigment-corpuscles. These touches are generally slightly curved, and appear to form two groups in each fin, a feature especially seen in the dorsal. The tail is faintly tinged with green.

The gall-bladder is deep green; the oil-globule is colourless.

In the mid-water net, on 9th April, a few miles from shore, the next stage, fully 6 mm. long, appeared. In spirit it presents a few black chromatophores on the cheeks, and the bases of the pectorals show the black pigment-rows present in the older stage (Pl. XVIII. fig. 11). The sides of the body from the tip of the pectorals backward almost to the tail show a series of isolated black chromatophores arranged in a double row, toward the dorsal and ventral edge. A group of similar pigment-corpuscles characterises the median or wide part of the marginal fin dorsally and ventrally. On the sides and ventral surface of the abdomen the same black chromatophores are scattered, and they run along the ventral surface to the base of the tail.

The marginal fin has expanded dorsally and ventrally in the median line, but only embryonic fin-rays occur in it. A slight narrowing dorsally and ventrally is evident in front of the tail, which also shows embryonic rays. The anus is very prominent, and in front of it another projection of the edge occurs—a feature characteristic of the form. The large pectorals likewise show only embryonic rays, and the lines of black pigment spring from the distal edge of the basal process. The notochord is quite straight.

The next stage observed was an example five-eighths of an inch in length, procured in

the mid-water net on the 28th April. The chief coloration is fine chrome-yellow, especially on the pectorals, spicules, and dorsal fins (Pl. XVIII. fig. 10). The pectorals are even larger, and the yellow pigment follows the line of the rays, with black points here and there, the intermediate region being yellow and black. The spines generally are large, those along the sides forming hispid rows, especially when looked at from the dorsum, and extending from the pectorals to the tip of the tail. The other features, which are chiefly those of the adult, have been indicated in a description published in the Fishery Board's Report by one of us.*

Callionymus lyra, L.—The ova of the skulpin, both ovarian and mature, have been described in another place,† but they have not, as yet, been hatched.‡ By the aid of the large mid-water net, a large series of young examples of this species, ranging from about 3 mm. to 10 mm. in length, were procured in August 1886.

In the earliest stage (a little over 3 mm.) the body is characterised by the great size of the head and abdomen, and the attenuation of the caudal region. The head is very deep, and the projecting mandible passes upward at a marked angle. The premaxillary region is not yet much developed, and the mouth has not the protrusible character distinctive of the adult. The body rapidly tapers behind the abdomen, and forms a slender, straight, almost whip-like continuation bordered by the membranous larval fin, with its embryonic fin-rays. The head and body are speckled with brownish-black pigment-corpuscles, which attain their greatest development on the ventral surface of the abdomen—a part usually pale in fishes. The pectorals are small, and no ventral fin seems to have been developed. The armature of the operculum, so characteristic of the more fully developed stage, is as yet absent. The stomach at this stage contained fragments of minute Crustaceans, apparently Copepods.

In the next stage, though the total length little exceeds the foregoing, considerable progress has been made. A larger amount of pigment exists on the side of the body, especially behind the abdomen, and it extends, though sparsely, on the hyoidean surface in front. The premaxillary region is now slightly protrusible. The eyes are large and somewhat quadrilobate. The abdomen still projects prominently below; but posteriorly the body has much increased in thickness, and the slender tip of the notochord, instead of being free, now forms the upper region of the caudal fin, the long inferior cartilaginous fin-rays stretching beyond it. The embryonic fin-rays extend from the notochord both dorsally and ventrally, and also at the tip. The hypural region is thickened, and the epiural is marked by a small patch. Speckled pigment runs along the base of the ventral marginal fin. The pectorals are somewhat longer than in the

* *Ann. Report for* 1888, p. 267.

† *Ann. Nat. Hist.*, Dec. 1885.

‡ RAFFAELE thinks that the reticulated condition of these ova (see p. 15) was due to immaturity—that is, that such represented the follicular layer of the ovarian egg, since in the ripe ova of *C. festivus* they were not present. Mr J. T. CUNNINGHAM, however, has recently met with a pelagic egg, off Millport, in June, agreeing quite with our former description, which was taken from mature eggs (*vide*, *op. cit.*, p. 124).

[Since this paper was read Mr CUNNINGHAM again confirms the original observation of one of us in 1885.—*Jour. Mar. Biol. Assoc.*, N.S. i. p. 37.]

last stage, and a pale process or papilla indicates the presence of the ventral fins. The next stage to be noticed (about 5 mm. in length) shows a more regular fusiform outline, and from the increase of pigment along the ventral surface it is considerably darker than the dorsal. By the widening of the cheeks the eyes have become more oblique, so that they are largely seen from the dorsum, whereas in the earlier stage they were more in harmony with the usual piscine type. The forward growth of the premaxillary region, and the increased arch of the mandible, greatly alter the facial aspect. The ventrals appear as a pair of short fins below and in front of the pectorals. From the marginal fin the anal is differentiated inferiorly, and is separated by an interval from the caudal. The fin-rays are much more distinct in this lower fin than in the dorsal. The development of the hypurals has pushed the tip of the notochord upward, but it is still surrounded by the embryonic marginal fin. The inferior caudal rays far exceed it in length, and they spring from a vertical hypural edge. The shape of the tail is conical, broad at the base, and narrow at the tip. The opercular margin does not yet show spines.

When 1 or 2 mm. longer, the arrangement of the pigment is unaltered, the ventral surface and posterior region of the body being tinted somewhat deeply by stellate pigment-corpuscles, while the dorsum is less uniformly coloured. The body behind the abdomen is thicker, so that when seen laterally the fish is fusiform, though, viewed from the dorsum, the head and abdomen are still disproportionately broad. The pectorals and ventrals are larger, the former showing blackish pigment-specks on the fleshy basal region, and a few dark radii on the fan-shaped distal region. The under surface of the ventrals also exhibits dark streaks between the rays, and they are considerably shorter than the pectorals. In shape both pairs of fins approach those of the adult. The first dorsal is merely indicated by a few short processes. The pale second dorsal fin (the embryonic fin having disappeared) begins behind the middle of the back, and terminates a short distance in front of the caudal fin. From the anus the anal fin extends to a point below, and somewhat beyond the dorsal above, as shown by an imaginary vertical line. Between the rays very evident dark pigment-streaks occur, a feature in consonance with the development of pigment on the ventral surface. The tip of the embryonic tail has now coalesced with the upper lobe of the permanent caudal, and the latter is somewhat less conical as well as broader at its termination. In some of the more advanced specimens at this stage the opercular armature is present as a straight spine, with a spur—coming off nearly at right angles—toward the tip.

When the length of 9 mm. has been attained, the body is still stouter behind the abdomen, the ventral fins have gained greatly on the pectorals, so that though they arise considerably in front of them, their tips are nearly in a line with the extremities of the former. The fan-like pectorals have much stiffer rays, arising from the semicircular base. The opercular spines stand out on a long process, and their tips slightly incline towards each other, the margin between them being semicircular. The first dorsal is now distinct, and the anterior rays of the second dorsal are longer than the others.

When 10 mm. long, the characters of the adult are more evident, the telescopic mouth

at once attracting notice. The median rays of the pectorals have lengthened, yet the ventrals are almost as long, the tips passing beyond the anus. The fleshy pad at the base of the pectoral is pigmented, but otherwise both these fins and the ventrals are pale in colour. The first dorsal is still short, but the second dorsal and the anal fins are prominent. The caudal expansion is now truncated at the tip. The abdominal surface is still coloured with black pigment. When taken out of the water the dorsum is somewhat greenish, diversified here and there with black pigment just as on the occipital surface, at the first dorsal, on the posterior end of the abdomen, and in the form of two conspicuous wavy bands behind, *i.e.*, in front of the tail (*vide* Pl. XIX. fig. 11). The figure here referred to is from a sketch made some days after confinement in a glass tank in the laboratory, hence the coloration is modified. The abdominal region is pinkish, from the contained food. The eyes are lustrous and greenish. In the laboratory the young fish lay at the bottom, keeping the pectoral fins in active motion, while the ventrals were spread out like a pair of wings.

All the young forms above described were captured some distance from the bottom (though they occasionally occur close to the St Andrews rocks in August), and therefore the development of the fins after the disappearance of the embryonic membrane is in relation to this pelagic life. The remarkable duskiness of the ventral surface, which is pure white in the adult, is probably also connected with their temporary sojourn in the region above the bottom. The protective spines on the opercula are, it is interesting to note, very early developed. The vertebral column in the largest examples shows thin transparent ossifications of the surface and of the arches, but the centra are more or less notochordal. A specimen, 20·5 mm. in length, obtained from the stomach of a cod, still more closely resembled the outline of the adult, though the pigment had been removed by the gastric juice. The opercular armature of this example was well developed, presenting three large spines posteriorly (one passing backward and two upward), while one large and several minor spines occurred in front. We have found that the adults spawn in August, it may be somewhat earlier or somewhat later, and it is plain that all these young specimens cannot belong to the same period—cannot be, that is to say, merely a month or two old. Such a supposition would be inconsistent with what has been observed in the young from other pelagic eggs. On the other hand, if these are the young from ova spawned the previous August or thereabout, then their growth is somewhat slow, but probably some examples spawn much earlier than others.

Liparis montagui, Donov.—Shortly after hatching, which is easily accomplished even under unfavourable circumstances, the larvæ (Pl. XIII. fig. 1) move both tail and pectoral fins actively. The cuticle presents a finely reticulate appearance on the marginal fin, which everywhere has embryonic fin-rays, and a series of globular glands occur over this and the sides of the body. At a somewhat older stage (Pl. XVI. fig. 7) the yolk-sac is studded with stellate black pigment-corpuscles and touches of chrome-yellow, and on each pectoral is a large spot of yellow with black chromatophores, and then a narrow yellowish curved band with similar black pigment. A few chromatophores with remarkably elongate

processes form in a line along the ventral edge of the myotomes, but none exist on the dorsal. The eyes have a greenish iridescence like a diamond-beetle's wing. The notochord is quite straight at the tip, and its cells are large. The tail-fin presents only a trace of a dorsal enlargement. The nasal capsules form two conspicuous pits. The heart has a small oil-globule below it, and the large oil-globule lies immediately behind the heart—in front of the yolk, which is granular. No blood-vessel occurs in the tail proper, the aorta passing almost to the tip of the chorda, and bending upward and forward into the vein. The blood is comparatively pale, being only faintly pinkish in the heart. The vertical vessels (intervertebrals) running up the sides of the notochord are proportionally large. The branchial bars are cartilaginous. The liver is pale, and burrowed with large vascular channels, while the densely folded alimentary canal lies above it. It curves into the posterior region of the yolk-sac, and when the latter is viewed from the ventral surface a folded region of the gut is evident, but no external opening.

The larval form figured in Pl. XV. fig. 2, was supposed to be Montagu's sucker at an early stage, but it differs in the presence of dorsal pigment. Some variation, however, may occasionally occur. On the other hand, several species may have ova and larvæ very similar to Montagu's sucker. In this form the regularity of the vitelline vessels and their simplicity, as well as the large size of the cephalic vessels, are noteworthy.

Centronotus gunnellus, L.—Masses of ova* about the size of a Brazil-nut have more than once been found in cavities (holes of *Pholas*) at the Pier Rocks, with the parent-fishes coiled beside them. The examples specially dealt with occurred on March 14, 1887.

The egg-capsules examined were somewhat friable, as all the embryos had escaped. The zona has a finely punctate appearance, and the punctures are most regularly arranged. The lacerated margin, however, presents very fine crossed fibres, probably due to the condition of the specimens, and these fibre-like markings disappear in Farrant's solution.

The larva measures just over $\frac{1}{5}$ of an inch ($\frac{1}{5\,0}$). It is extremely translucent, and when hatched shows no trace of pigment, save that the pupil is dark (Pl. XIII. fig. 6). It is extremely hardy and active, darting through the water in various directions, and again resting on the bottom. The head is blunt and rounded. The auditory organs (*au*) are very large, the eyes moderately so. The most remarkable features are the extreme length and thinness of the embryo, its eel-like form, the great length of the alimentary canal (*g*), and the character of the yolk-protuberance (*y*), which is directed somewhat forward. The latter is not of great size, and the vitelline mass proper is of an elongated ellipsoidal shape with a faint opacity, and having in its anterior ventral part a single oil-globule (*og*) of crystalline translucency, very slightly tinged with ochre, and surrounded by a thick protoplasmic coat (*p*); while, from the shortness of the sac, the globule is near the heart. Entirely covering the posterior surface of the yolk is the liver (*lr*), which projects as a long cellular process from the abdominal region proper, and insinuates itself between the hypoblastic covering

* These ova appear to have been first recognised by Mr Anderson Smith on the West Coast.

of the yolk (*y*) and the thin yolk-sac (*ys*). The oil-globule (*og*) seems to lie in a pocket in the cortex of the yolk, as an equatorial line crosses over it, yet it is also enveloped by a complete protoplasmic covering (*p*). The gall-bladder (*gb*) occupies, in the upper posterior portion of the liver, a position just at the angle where the ventral embryonic fin (*ef*) joins the yolk-sac. As first shown by De Filippi,* the gall-bladder of the larval *Clupea finta* lies also behind the yolk; the liver, however, does not in this instance pass downward. The pectoral fin (*pf*) is somewhat fan-shaped, very thin and membranous, and stands erect; while a chitinous clavicle (*cl*) is fixed by a longitudinal lateral attachment. The long intestine, with a distinct rectal portion, curves downward a considerable distance from the yolk, and cuts off, by the anal protrusion (*a*), a ventral fin-area about one-third the length of the inferior embryonic membrane. The lumen of the alimentary canal is spacious and the walls much folded, but that of the œsophageal section is very much diminished. A valve or cincture marks the commencement of the rectum (*hg*). The segmental duct (*sg*) is plainly seen passing from a convoluted pronephric portion (with oval glomerulus, *gl*), with an undulating course to a spacious urinary vesicle (*uv*), which opens close to the anus (*a*). The notochord (*nc*) is fairly straight, but in the mid trunk it ascends by a gentle curve and gently bends round, to end between the posterior limits of the two eyes. It has the usual large irregular cellular structure, and presents a distinct perichordal sheath (*pcs*). The heart (*h*, Pl. XIII. fig. 5) is fully formed, showing a rounded ventricle, which gives off, in front, a narrow bulbus directed upward, and behind receives the large vase-shaped auricle, opening into a wide sinus venosus. The pericardial chamber (*pd*) is large, and its floor is entirely free from the yolk.

The oral and branchial cartilages are well developed (Pl. XIII. fig. 5). The mouth is widely open on emergence, and water freely enters. Only tremors of the mandible, however, are noticed. The mandible (*mn*) is as usual a massive cartilage with an enlarged articulating extremity, joined by two cartilages from above, the anterior or quadratopterygoid (*ptg*), and a more massive hyomandibular (*hm*), which springs by a large base from the floor of the ear-capsule (*au*). Four acutely curved branchial cartilages (*bra*) are present, and the long hyoid cartilage (*hyd*) ends in a copula, which projects as a nodular eminence on the under surface of the mouth. The maxillary elements cannot be made out, but the front margin forms an overhanging upper lip. The parts of the brain are well marked,—the fore brain (*fb*), on the lower anterior face of which are laterally placed the nasal sacs (*ol*), the pineal gland (*pn*), and the large dome-shaped mid brain (*mb*), with the cerebellar fold (*cb*) behind. The eyes have a silvery lustre, with a black pupil. A few black pigment-corpuscles occur over the anterior superior curve of the eye, and this region shows a fine green shade like malachite.

The structure of the ear is very complex, and the two otoliths seem to lie in the same anterior ampulla.

The marginal fin (*ef*) commences very gradually between the ears, *i.e.*, posterior to he cerebellum, and it does not become very wide, although its depth is somewhat increased

* *Ann. des Sci. nat.*, 3me sér., vii. p. 66, pl. i. fig. 1.

over the anal region and at the tapering caudal extremity. In this latter portion embryonic striations or rays (*er*) appear, and are especially distinct in the upper portion.

In a fortnight the changes were the appearance of very finely stellate pigment over the corrugated rectum (*hg*), and between the latter and the urinary vesicle (*uv*). Smaller stellate pigment-spots proceed along the ventral surface of the gut to the yolk-sac, but they go no further. The same stretch behind the vent along the edge of the muscle-plates. Two or three stellate pigment-corpuscles also appear over the yolk-sac, about midway between the oil-globule and the notochord. In some the yolk has considerably diminished, and the oil-globule is thrown rather more to the front. The ridge from the ventral marginal fin goes a considerable distance forward over the yolk-sac.

In a few days the young fishes exhibited a tendency to lie on their sides at the bottom of the vessel.

After the lapse of five weeks, the majority of the larvæ (Pl. XIII. fig. 7) had the tendency just mentioned. A well-marked interrupted line of pigment runs from the cardiac region to the anus, passes forward and upward behind it, and is then continued to the tail. The marginal fin is continuous from the anus to the tail; a narrower fin occurs in front of this, and it diminishes about the region of the gall-bladder, which is large and distinct. The dorsal fin again is similar, and deepens only a little in front of the caudal, which in outline is somewhat lobate. The fin-rays are present in the tail, and are at this time better marked in the ventral (anal) than the dorsal fin. They are also distinct in the pectorals. The snout now extends forward about half the diameter of the eye in front of it; and the mandible projects a little further, but is motionless, the animal aerating its gills in its progress through the water. The lateral view of the head much resembles that of the cod or gurnard at a similar stage, but the diagnostic features besides those mentioned are the great length of the body and the median position of the anus. In the tail a hypural thickening has taken place, with a few coils of vessels which show pale blood coursing through them. The large size of the otocysts, and their continuation upward so as nearly to meet in the median dorsal line, is interesting.

Most perished at the end of April from impurity of the water, but such as survived showed little change in habit and structure.

Young gunnels, $1\frac{1}{2}$ inch long, having the external features of the adult, were procured in July.

Lophius piscatorius, L.*—An injured example of the post-larval frog-fish was procured by means of the mid-water net, 15 miles off the Isle of May, on 30th August 1886, at a depth of 25 fathoms, on 32 fathoms' ground. Its length is 7 mm. In outline it presents (Pl. XIX. fig. 6) a large flattened head and a slender body, the notochord at the tip of the tail being bent upward at the dorsal angle. This curved terminal portion

* The rarity of the floating ova of this species on the east coast of Scotland is remarkable, for the adult is very common in stake-nets and trawls. So far as known, the spawn is also uncommon on the west coast, though there and off the south coast it has once or twice occurred recently. A specimen sent to the Fishery Board was stated to be the ova of the cat-fish. Raffaele failed to meet with it in the Bay of Naples.

has still the embryonic fin, and the adjacent part of the dorsal fin is long. The fin-rays proper (inferior) are well marked and long; and the outline of the tail is thus peculiar. The specimen, though apparently younger than the last stage figured by Alex. Agassiz (*op. cit.*, pl. xviii. fig. 2), if the condition of the tail be a reliable point, yet diverges very much from it: still more does it diverge from the older stages of Günther and Day. The head forms an expanded flattened plate, rounded in front from the marked premaxillary curve, and with a median notch; while behind lie the two nostrils, a little distance on each side of the middle line. The large eyes are situated more than their diameter behind the anterior margin of the snout, and less than four (about three and a half) of them would give the greatest transverse diameter of the snout. They are thus large and prominent, and look directly upward. The cranial and other cartilages have a covering of transparent hyaline bony tissue. Behind the eyes the body narrows to a slender region, which is barely twice the length of the head. This region still carries the embryonic fin dorsally and ventrally as a nearly uniform fringe, with the true fin-rays developing in it, though in the anal portion (ventral border) the marginal fin here and there retains its original condition. The other fins present in the specimen are a pair of enormous pectorals attached to the great shoulder-girdle, a plate passing transversely behind the branchiæ. The ventrals are situated in the middle line just at the anterior end of the pectorals, but both the former are injured. They are very short, but the rays seem to have been broken; yet, allowing for this, they appear to be little developed. The anterior fold of the pectorals runs in front of these fins externally. The great changes that must ensue during development in regard to the gill-slits and the situation of the pectorals are noteworthy, while the ventrals remain almost in the same position. The under surface of the head is marked by the expanded hyoidean apparatus and the slender mandibular bars, the symphysis of the latter forming a sharp angle in the preparation. The gills are three in number, and the gill-slit is large and long, extending from the dorsal margin to the anterior ventral attachment of the branchiæ. The branchiæ have simple papillose processes. In the stomach were small Copepoda and larval Crustaceans.

XII. General Remarks on Post-Larval Fishes.

Variability in the size of young marine fishes of the same season is one of the most conspicuous features in their history, and probably depends on the earlier or later period at which spawning takes place. Moreover, it is evident that in those species spawning by degrees considerable differences in size will occur, in the same fish, between the products of those ova shed first and those which issue last. Some species, for example the cod and the sole, seem to have annually a very extended spawning season, the sole commencing in May off the east coast, and continuing till August. The fact just mentioned is demonstrated in a single sweep of the mid-water net on suitable ground in

autumn when swarms of little gurnards are captured, the smallest of which are very little larger than those reared in the laboratory, while others are three or four times longer.

Moreover, experience of fishes such as the salmon, in which all the ova issue nearly simultaneously, shows us that the growth of the young of the same fish is variable, many being larger than others at a given time; some, for instance, becoming smolts at the end of the first year, others not till the end of the second. Further, during the second year great disparity occasionally exists amongst the young fishes.

When we come to survey the condition in the cod, the problem is more complex, since the material is less abundant and more difficult to obtain. Statements had been made by various authors about the life-history of the cod, but these were both vague and incomplete; Prof. G. O. Sars, indeed, as already indicated (p. 153), was the first to produce a definite and satisfactory account of certain stages. He, however, found no intermediate links between the larval form of 6 mm. and the post-larval form 24 mm. in length, the former occurring on 28th May, the latter on 12th June, and the most recent remarks of Ryder leave the same gap. The spawning period of the cod, therefore, would appear to be later in the Norwegian waters. It occurs as a rule in April in the British seas, though a margin must be given on both sides of this period,* and the larval cod abound in the surface-waters in areas frequented by the adults at the time. Towards the end of the same month, however, small Gadoids occur in St Andrews Bay, the least being about 6 mm., so that it is possible such represent a post-larval stage from early ova. Others again are double the length and upward, indeed there is great variety. These small forms are met with amongst the others throughout the summer, and generally occur in the mid-water net rather than in the trawl. On the 1st of June, however, the distinctive coloration of the young cod (now $\frac{1}{16}^{5}$ in. in length) is recognised, in a rudimentary condition, and subsequently there is no difficulty in following it. They occur in the trawl, and at the margin of the tidal rocks.† Now, can we assert that all these are the young produced from the ova of cod which spawn in April? At first one of us was disposed to think that those which appear in shoals off the rocks in June, and which are about an inch in length, were those of the previous season, since it would be difficult to explain this remarkable rapidity of growth if the spawning period (viz., April) be correctly stated. Though the latter rests on proved observation, yet it must be borne in mind that the limitation of the spawning period to April is arbitrary, and it may only reach its culminating point then. This consideration, and the remarks formerly made as to the causes of variability in size, may, when coupled with great rapidity in growth, form the whole into one continuous series of young cod of the season. Such has been rendered more probable by the occurrence of the smaller forms early in April as well as subsequently. Moreover, a change of area apparently takes place to some extent, since the mid-water net shows that these post-larval cod only appear in the Bay in April and May.

* *Vide* "The Pelagic Fauna of St Andrews Bay," *Seventh Annual Report of the Fishery Board for Scotland.*

† As shown in the *Report on the Pelagic Fauna*, the sizes of the pelagic young-food fishes captured in the mid-water net does not increase as the season advances, apparently for the reason that the large forms go downwards as they grow.

The net is small enough to capture larval cod, but they are not a conspicuous feature, very few having been seen, and the intermediate stages between the larval form and the post-larval are difficult to obtain. The latter apparently tend shorewards in the end of April, not at the surface, but in the deeper parts of the water, many, indeed, being by and by caught on the bottom by a fine trawl-net. They sport about amongst the tangle-forests and shallow water and neighbourhood, and as they get older seek the deeper parts near the rocks.* They then, as Sars says, form shoals in deep water on the various fishing banks, large numbers being caught the following summer both by liners and trawlers.

That a migration occurs in other Gadidæ is apparent when we consider the case of the ling. As a rule, the old ling frequents the deeper parts, yet the young, ranging from 5 inches upward, are plentiful off the Pier Rocks at St Andrews, especially in their barred or tesselated condition. The post-larval haddock also would appear to frequent the deeper water, as also does the post-larval whiting, the latter occurring in considerable numbers south-east of the Island of May, and at a later period than the post-larval cod. When older, viz., from 3 to 6 inches, they are not uncommon in St Andrews Bay at low water. The larval frog-fishes and other types follow the same habits.

On the other hand, some of the ordinary Pleuronectidæ, *e.g.*, the flounder, take a somewhat different course. The larval forms are pelagic on the sites† frequented by the adults, and then they gradually seek the bottom as well as the tidal margin, especially the mouths of streams, in May, June, July, and August. They may be found in lessened numbers there till well grown, so that the migration of this form is slight. The young plaice appears to follow similar habits, but the large adults seek the deeper water off shore. The same may be said of the turbot, the brill, and the long rough dab. The larval forms of the craig-fluke (*Pleuronectes cynoglossus*) frequent the ground occupied by the adults, and various stages may be secured by the same haul of the net. On the whole, then, the evidences of migration relate only to the passage in certain species of the post-larval stage to the shallower water, and the tendency of all the healthy larger forms to seek the deeper water. The latter feature, for instance, is observed in the halibut. It is apparent, however, that certain flat fishes, *e.g.*, the "witch" or craig-fluke, so far as at present ascertained, are confined for the most part to the deeper water and soft ground, both in their adult and their younger stages; and Müller's topknot, the lemon dab (to some extent), and others probably agree with them in this respect. It appears to be a feature of moment that the post-larval forms of such as the "witch" and long rough dab swim somewhat longer on edge—that is, are larger fishes with great depth of body before the eye travels round, and before settling on the bottom. The post-larval stages of the flounders and plaice appear generally in April, and are about half an inch or less in length, their eyes as a rule being lateral in position; and as the season advances the left eye moves forward a little, and approaches the dorsal edge. They vary considerably in size at a given time, but not so much as the "witches" formerly alluded to, and would

* *Vide* No. 104, p. 309.

† Generally inshore.

appear to seek the tidal margin with great rapidity. The flounder and plaice are probably the first to appear, the common dab being a little later. All the shallow sandy flats round the British shores abound with young Pleuronectids.

The Clupeoids of the first series appear in great numbers in the Bay in March, and their presence corresponds with the period at which the hatching of the eggs of the herring was accomplished in the laboratory. The comparative rate of growth was followed thereafter in the Bay throughout the summer months. Thus they measure about 7 mm. in the early part of March, 12 to 15 mm. a month later, and in two months about 20 mm., with a great increase in depth. In four months (*i.e.*, from March) they reach 27 to 28 mm., though such may be small examples of this (the first) series. Those of the second series occur in September and the following months.

Though the differences existing between the larval herring and the larval sprat are marked at the period of hatching, the former being a much larger and more active fish, which soon gains strength to mount upward in the water, the latter being shorter and furnished with a larger yolk, yet the rapidity in growth soon obliterates the most evident features. Thus no bold line of distinction, as regards increase and safety, can be drawn between these closely allied forms with their dissimilar eggs. Each is as prolific as the other, and holds its own in every part of our seas. Much, no doubt, remains to be discovered in this and similar cases of divergence of the ova of closely allied species, but at present no general law can be laid down on this head, or in regard to the occurrence of oil-globules. It is difficult to explain why the brill and Müller's topknot should have an oil-globule in their pelagic ova, and the turbot and "witch" be devoid of it.*

The larval forms associated with the sand-eel occurred at the end of March, their length being 6 to 7 mm. At the same time, however, larger forms were captured, viz., 18 to 25 mm. On the 14th April they had reached 8 to 9 mm., and at the end of the month 14 mm. at most. On the 7th May others measured 27 mm., 10th July 33 mm., and in August 45 mm.

When placed under favourable conditions, there is no doubt young fishes grow rapidly, as in the case of the viviparous blennies, which before leaving the ovary of the adult reach the length of nearly two inches.

While there is no difficulty in rearing large numbers of food-fishes to a certain stage in the laboratory, it is probable that it would be most convenient, when stocking certain bays, to place the larval fishes in the sea within a week, for thus they would be furnished with more abundant, more varied, and more suitable food. Further, the introduction of adults ready to spawn (*e.g.*, soles) in suitable sandy bays, would probably be found more economical than the method indicated, and they can be carried long distances with ease and safety. The same remark applies to the herring, for adolescent examples accustomed by degrees to fresh water, can thus be carried without injury to distant regions.

* Mr Cunningham (*op. cit.*, 1889, p. 48) has recently broached the hypothesis that the presence of an oil-globule in the egg is connected with abundance of oil in the adult. This would not seem to suit in contrasting the turbot with the brill, the cod with the ling, the bib with the gurnard, the dragonet with the rockling, &c.

Monstrosities.—Abnormalities of a marked kind were not frequent in the marine larval fishes hatched in the laboratory. Amongst these observed, however, were a double-headed example of *Pleuronectes limanda* (Pl. V. figs. 3 and 3*a*, *in ovo*), the latter figure being taken three days later than the former, and when the pigment had appeared. A cyclopean embryo of *Trigla gurnardus*, again, is represented in the same Plate, fig. 5, other abnormalities being present in the ovum. An abnormal tail of the same species, referred to elsewhere in this paper, is also shown on Pl. XIV. fig. 3. The notochord with its investment continues in the axis of the body, while the caudal region bends separately to the left.

XIII. *Anarrhichas lupus*, L. The Wolf-Fish. Development and Life-History, with Remarks on the Salmon and other Forms.

Intra-Ovarian Ova.—The intra-ovarian ova of the wolf-fish had been met with occasionally during the work for H.M. Trawling Commission, it being stated in the Report that they were of considerable size in February, and that at this period an abnormal example of a large ovum (which had not been discharged) was observed. In August, again, the ova were more than an eighth of an inch in diameter—in fact, it was clear that the spawning period of this fish was late, and in contradistinction to the published views on the subject. Thus, Day * mentions that, "according to Pennant, it spawns in May and June, when it deposits its ova on the leaves of marine plants; the fry are of a greenish colour." Parnell, also quoted by this author, states that "about June the young are 2 feet in length." † That it could not spawn in May or June was evident by an examination of a specimen 3 feet 1 inch long. The ovaries were 6 inches long and about $1\frac{1}{2}$ inch in transverse diameter as they lay on a flat surface, connate from the posterior end forward nearly a third of their length, and fixed by strong membrane in front of the fork. The ova form dense masses along the inner edge of each ovary, the great bulk of the eggs occurring there, for those on the rest of the surface were less numerous. The majority of the eggs are nearly of equal size, viz., about 1·5 mm., and each is invested by a vascular follicular membrane with very fine epithelium. Amongst these, however, many minute ova (visible to the naked eye) occur, and ranging from ·75 mm. downward. In these the capsule is thick, the contents coarsely granular, and the nucleus large. A single large egg, about 6 mm. in diameter, and with an oil-globule 1·75 mm., was present, having evidently been retained after the others had been shed, as occasionally happens to other fishes—both marine and fresh water. The arrangement of the ova along the inner (*i.e.*, median) border of each ovary was lamellar, masses of eggs hanging from the wall, so that it was on the whole roughly fimbriated. Minute blood-vessels covered each egg and the intervening membrane. In the very early stage the ovum lies in a capsule in the epithelial membrane of the ovary, and shows a large nucleus and nucleolus; while the

* *Op. cit.*, p. 196. † *Fishes of the Firth of Forth*, p. 240.

contents of the egg are finely granular. The usual changes take place, the nucleolus disappearing, and by and by, when the egg reaches 1 mm. in diameter, only coarsely granular contents are present. Before deposition the yolk clears up and the oil-globule becomes conspicuous.

The earlier stages of the extra-ovarian development of the wolf-fish have not yet come under notice, for the ova procured on 16th January 1886 had reached an advanced stage, the embryos being considerably developed, and showing not only abundant pigment in the anterior dorsal region, and in the eyes, which had a silvery sheen, but an active vitelline circulation. The movements of the embryo within the egg-capsule, too, were frequent and vigorous. It was necessary to tear the large mass of adherent ova in order to place them in the glass vessels of the laboratory, and a few embryos were thus set free. During the next four or five days many spontaneously emerged, but the appearance of those which escaped on the 23rd or 24th of January presented no noteworthy advance on their predecessors. The larval fishes at this date measured 11 or 12 mm. on emerging. The translucent body (Pl. XX. fig. 2) is comparatively slender, and is surrounded by a delicate and continuous marginal fin. In the lanceolate caudal region a slight dilatation occurs. The yolk is bulky and of a translucent straw-yellow hue, and a large oil-globule of a dull yellowish tint is present. The coverings of the sac show finely granular cells with large nuclei (Pl. XXI. fig. 5). The pectoral fins are in constant motion, just as those of the young salmon are, and yet it is doubtful whether the young wolf-fishes here referred to did not escape prematurely. Some had difficulty in escaping from the zona radiata, a circumstance noted, however, at a much later stage, when the head and yolk-sac frequently remained enclosed, while the tail alone was free.

The favourite position of the most vigorous larvæ is on edge (Pl. XX. fig. 5), the rounded pendulous yolk resting on the bottom of the vessel, and thus steadying the young fish, while keeping its head above the sand or sandy-mud. The large oleaginous globule is situated on the anterior face of the yolk, a short distance below the head, and may possibly aid in maintaining the sac in the position just indicated. The situation of the globule is characteristic, for in no other British Teleostean has this precise position been noted, nor does Agassiz indicate it in any American form, though, in his conjoint work with Whitman, an unknown embryo (not unlike *Cottus*) is represented with a small oil-globule behind the cardiac region. F. Raffaele,* however, has quite recently shown that certain Mediterranean forms, such as *Mullus* and *Coris*, have pelagic larvæ which bear the oil-globule at the tip of the prow-like yolk. The feature is interesting, as this body in most forms in which it has been observed is situated towards the posterior border of the yolk-sac, as, for instance, in another form, viz., *Lophius*,† frequenting like *Anarrhichas* the sea-bottom. When viewed from above (Pl. XX. fig. 5), the globule projects just in front of the snout, the great vitelline

* *Abdruck aus den Mittheilungen aus d. Zool. Stat. Neapel.*, Bd. 8, Heft 1, pp. 20, 35, tav. 2, figs. 5, 6, and 18, 1888.

† It must be noted, however, that *Lophius*, unlike *Anarrhichas*, has a pelagic ovum (*vide* Agassiz "On the Young Stages of Oss. Fishes," *Proc. Amer. Acad. Arts and Sci.*, vol. xvii., 1882, pl. xvi. fig. 3).

vein passing upon the right, and in some a distinct bulging of the yolk-sac occurs in front of the globule. Moreover, during the extremely cold weather of the period, the globule was often thrust outward at this part. The head of the embryo presents a remarkably truncate appearance, the snout, indeed, projecting less than the large eyes, when viewed from the dorsum (as in the figure just mentioned). A decided difference exists, therefore, in this respect, when compared with the young salmon, in which the long yolk-sac trends downward and backward, whereas in this form the yolk-sac is globular, and is directed downward and forward.

This being, so far as known, the largest British marine Teleostean larva yet described, its comparison with that of the salmon, the largest fresh-water form, is naturally suggested. Many points of contrast are at once presented; thus the difference in coloration is marked, for while both have pigment in the eyes, the yolk in *Anarrhichas* is straw-coloured and inconspicuous, whereas in the salmon it is rendered conspicuous by the deep reddish-orange colour of the oleaginous globules. The latter become grouped, again, in masses in the upper region of the yolk-sac; whereas in *Anarrhichas* the single, large, somewhat lenticular globule maintains a constant position in front. The general pinkish tint of the newly-hatched salmon, further, is more pronounced. The external features of the wolf-fish also present less differentiation, for the marginal fin is simple and continuous, the tail is lanceolate, and the pectoral fins at this stage are much smaller. The head, moreover, is very different, for when viewed from the dorsum (Pl. XX. fig. 5), the large eyes, as already noted, project even further than the snout; while in the salmon the snout protrudes considerably beyond the eyes.

In a newly-hatched example about a week later (1st February) the tail is somewhat bluntly lanceolate, the ventral lobe being more distinct than the dorsal (Pl. XX. fig. 1), and the notochord passes in a straight line backward to terminate in a point. A slight wrinkle of the margin of the delicate caudal membrane occasionally marks this termination. The notochord here is finely cellular, the size of the cells increasing anteriorly. The neurochord presents a marked diminution just above the margin of the vascular loop beneath the notochord. The membranous tail-fin has fine striæ (embryonic rays, produced by delicate fibres), and is cellulo-granular. The aorta, in coursing backward, gives off a twig inferiorly, which diverges from the ventral surface of the notochord, and then ends in a slender vessel passing almost to the tip of the chorda, and returns as a recurrent vein. The ventral twig of the aorta splits into two loops, which ramify over a limited area (see Pl. XX. fig. 1), and then joins the caudal vein by a single trunk. This condition diverges from that in the salmon at the same stage, but a comparison between the two forms may be conveniently reserved till a later period. The circulation in the caudal region attains but a slight development in the wolf-fish at this stage, whereas the vitelline vessels are as fully developed as in more advanced larvæ.

Vitelline Circulation at the Period of Hatching.—We have already mentioned that on emerging a large vitelline vein passes on the right side of the larval trunk, collecting

the blood returning by two main branches—the afferent trunks from the liver carrying a stream downward posteriorly and joining the posterior division, the other great branch receiving its supply from the opposite side (Pl. XX. figs. 4 and 5). Considerable gaps, as regards the larger trunks, occur on each side of the vitelline vein and below its branches at this stage, but examples somewhat differ from each other in this respect. These trunks are all, even the smallest, of comparatively large calibre, and appear in ordinary views to be hollowed out of the yolk, and without the distinct walls of typical venous trunks. The vessels frequently anastomose with each other, and their general direction is downward and forward. Some of the upper twigs (in larvæ of 22nd February) pass rapidly across the yolk-sac to join the main vein, above the oil-globule. When the fish is in a dying condition the current becomes less swift, and frequently recoils in the vessels, but especially in the great vein. On the left side (Pl. XX. fig. 2) a great trunk from the liver courses along the anterior hepatic curvature, while several smaller but still considerable trunks issue from the same organ posteriorly, and rapidly break up into many branches, forming a complex network over the posterior half of the sac. Their terminal branches join a large and nearly horizontal trunk, which slants slightly upward and forward to join the vein. The divergence of this arrangement from such a species as represented in Pl. XV. fig. 2, from ova resembling those of Montagu's sucker, is marked, the vessels in the latter being few and short, and having a comparatively straight course.

About a month later (Pl. XXI. fig. 2) the complexity of the circulation on the left side has increased. The anterior vessel of the series issuing from the liver, which curves downward and forward—branching as it goes, has become much larger.

On 1st April, again (about 5 weeks later), the chief change since the former period is the great size of the anterior trunk (marked *a*, Pl. XXI. fig. 2) and its shorter course. The vessels to the right (that is the posterior vessels) are diminished, and they have a decided slope to the front. The slope, however, is much less marked than on the right side. In the most advanced forms at this time (Pl. XXIV. fig. 7) the alteration in the direction and size of the vessels of the yolk is remarkable. Thus, on the right side, the main part of the blood is conveyed by a large trunk passing to the posterior border of the liver—slightly downward and forward (though the course may vary) into the great vitelline vein, a little below the heart. This blood does not, therefore, pass over the sac. Some of the vessels of the yolk seem to have diminished in size. The great trunk just alluded to is twice the size of that in an example in which the yolk is still very large (*i.e.*, a younger specimen), yet each, though so unequally advanced, may have emerged from the ovum almost at the same time. Of course, the diminution of the yolk-mass enables the larval-fish to swim more readily through the water. It must be noted that the direction of the trunks detailed above may, as indicated, vary considerably, for in one example two large trunks issued from the front of the liver, then rapidly curved toward the anterior border and joined the efferent vein. The rapidity of the current in these two main trunks is in contrast with the steady and slow current in the branches covering

the surface of the yolk, and though a large posterior vessel shows a more rapid flow than the rest, still it is not so swift as in the anterior trunk. The great anterior vessels have a shorter and more nearly horizontal course, and do not wander over the yolk as observed in February.

The blood-discs of the wolf-fish present no special feature of note, though they sometimes undergo peculiar changes of form after escape (Pl. XXI. fig. 5*a*).

In about a fortnight after hatching, the yolk-sac has materially diminished, forming a rounded projection anteriorly, somewhat less in bulk than the head above it. In the example studied, the globule was found to have passed to the right side (Pl. XXI. fig. 3), and a considerable portion of the yolk-mass lay in front of it. The vitelline vein was thus carried backward by the peculiar displacement of the oil-globule. The smaller vessels curved round the anterior border of the globule to join the vein or its branches at various angles, but in the main more or less transversely. A similar arrangement occurs posteriorly, though the branches may, in lateral view, often have a shorter course, since the great vein is, inferiorly, nearer the posterior than the anterior border. On the left side (Pl. XXI. fig. 3*a*) the anterior vessel is now superior in position, and is somewhat transverse in direction, while the other branches are much shortened, and their course is chiefly downward and forward. In those most advanced (Pl. XXVII. fig. 1) the yolk-mass is noticeable only as a projection in front, for the posterior end merges, as it were, in the abdomen. The oil-globule now lies under the branchiostegal rays. It is noteworthy that the absorption of the yolk was accomplished in some cases at the beginning of May. Moreover, while the young fishes were comparatively delicate in their earlier stages, an alteration seemed to ensue about the time of the absorption of the yolk, so that they became more hardy—their tenacity of life being so great that examples appeared to suffer little though left unchanged for some days in a very small quantity of sea-water.

We have explained that the outline of the yolk-sac in *Anarrhichas* is quite different from that in the salmon, being spheroidal instead of elongated and sloped posteriorly. It corresponds, in fact, rather to the condition in the embryonic salmon before hatching —say the 40th day in those which hatch on the 60th day. The shape in the salmon also shows the changes of outline during absorption more boldly, the sac in the healthy fish (Pl. XXII. fig. 4) becoming gradually attenuated posteriorly (*Ibid.*, figs. 7 and 8), and occasionally in the more vigorous specimens, as Sir J. Gibson Maitland has shown, a portion of this region is constricted off and shed. Such a condition is not possible in the spheroidal yolk of *Anarrhichas*. Further, the great abundance of oleaginous globules in the upper part of the yolk in the salmon, and the occurrence of smaller globules throughout the entire mass, is wholly unlike *Anarrhichas*. In the latter species the single large oil-globule is nearly constant in position, but in the salmon this is certainly less so, though the oleaginous spheres are towards the upper region, and often on the right of the embryo, yet during absorption of the yolk they become more or less posterior in position. At no period does the globule in *Anarrhichas* pass backward other than the slight degree shown

in Pl. XXI. fig. 3, a feature probably due to position under examination. The relation of the large globule to the position of the respective larvæ when at the bottom of the water is not perfectly clear, though there is reason to believe that, in *Anarrhichas*, as already pointed out, it is directly connected with the attitude assumed by the larva when at rest. Young salmon lie on one side amongst the gravel in their early stages, or occasionally rest with the yolk-mass dipping between the pebbles on the bottom, so that a definite position of the oil-globules in front would appear to be of little importance. The contained fluid, or deutoplasm, of the yolk-sac seems to be similar in both species. When discharged into the water it is transparent, viscous, and very tenacious. After a time it becomes solid, and of an opaque white hue like a stratum of tallow. In the salmon it presents in the latter condition abundance of dense oily globules, with adherent granules, resembling nucleated cells. In the large globules, however, the granules form only a superficial fringe. In some cases the oily matter, on escaping, sinks to the bottom of the water. Two kinds, indeed, of this matter are present—(1) orange-tinted oil, which floats at the surface, and (2) minute particles of oil imbedded in and held down by granular substance. When pressure is applied to the large globule it divides into two or more portions, so that it would appear that no definite protoplasmic investment encircles it. It also occasionally passes to the fundus (Pl. XXII. fig. 7), and sometimes its surface is slighted fissured. Some of the oil-globules appear paler in colour than others of the same size. The large globule is observed to persist almost till the posterior process disappears from the yolk-sac (Pl. XXII. fig. 9). Externally the latter in the salmon is covered by a layer of nucleated tesselated epithelium, the nuclei having nucleoli, and beneath is a fibrillated coat, below which the vascular layer lies. In hernia of the yolk-sac, the free portion presents a striated appearance, due possibly to the protrusion of the vascular (yolk-hypoblast) through the non-vascular layer, for in one example blood-vessels proceeded quite up to the margin of the hernia.

The walls are contractile, for the sac shrinks towards the body of the embryo on the escape of the contents. So also the walls contract during the gradual absorption of the contents of the sac, as observed at the end of the first week (Pl. XXII. fig. 6). As the organ shrinks, obliteration of the smaller and then closure of the larger vessels takes places. By and by (about the 13th day) the anterior region of the sac becomes flattened, so that it forms merely a slight swelling on the surface; and sometimes a few carunculi appear at the fundus. At the end of the third week the vitelline vein as well as the yolk-sac is much diminished. About the end of the fifth week the latter forms only an abdominal swelling, and is streaked with bars of pigment, which are directed downward and backward.

A glance at the figures of the sac during its later stages in *Anarrhichas* will show that the absorption takes place in a different manner from that just detailed, since instead of the final prominence being posterior as in the salmon, it is in *Anarrhichas* anterior, and the large oil-globule in the latter likewise is in the same region.

In regard to the circulation in the yolk-sac, the great vitelline vein in the salmon is

in front, and in its course upward it receives several large branches, but in the wolf-fish it is generally on the right. SHAW'S figure* shows the vitelline vein in the salmon occupying an unusual position; the yolk-sac, moreover, is too small for a salmon one day old, and the oil-globule should either be larger, or be represented by several smaller ones. The general direction of the small branches is transverse or oblique, the uppermost appearing at the posterior margin, and coursing obliquely downward and forward, the middle being nearly transverse, and the lowermost transverse and then upward. The last main branch collects the blood from the upper part of the sac, and enters the great vessel from behind, not from the ventral side.† In *Anarrhichas*, on the other hand, the left side has its twigs mainly at right angles to the body. The two large trunks of the vitelline veins pass from behind forward and upward to form by their junction the great venous trunk, and it is their disposition that gives a character to the vitelline circulation, in contrast with that of the salmon. The afferent vessels stream downward into these on both sides of the sac, those on the left, however, entering the great branch by numerous trunks (Pl. XXI. fig. 2), and thus forming a contrast to the right side (Pl. XXII. fig. 3). It is interesting that, after forming a *rete* on both sides, the smaller trunks should again join to form larger vessels which empty themselves into the main branch of the side, as shown in the figures above mentioned. The current in the smaller wavy trunks becomes slow, thus probably enabling those changes between the contained blood and the neighbouring parts to go on efficiently, and on being accomplished the rapid return of the blood to the heart is facilitated by the formation of the larger secondary trunks which join the great veins on each side. This arrangement is not seen in the salmon, though the vessels do not branch much, and enter the vitelline veins by a current not more than two or three blood-discs broad. In both species the supply to the sac is posterior, while the returning blood passes anteriorly.

The absorption of the sac in the wolf-fish took place about the middle of May, so that in all probability it occurred at a period similar to that in the salmon. The difficulty in preserving special examples, and the great irregularity in the conditions at birth, made the exact determination of the period uncertain. The young wolf-fish, like the young salmon, exhibits increased swimming power as the sac becomes less, shooting upwards into the water at first with a wriggling motion, but later as the sac diminishes it swims more steadily.

In the partial stasis preceding death the vessels of the sac are greatly enlarged, so that either the walls of these canals are contractile, or there is a great pressure of blood, and the latter certainly occurs from the slow rate of progress along the vessels.

Circulation in the Trunk.—The circulation in the larvæ which emerged in the middle and towards the end of January showed for the most part the ordinary Teleostean features. The main points will be detailed in comparison with the salmon, at a somewhat later stage, and, meanwhile, the condition on emerging may briefly be indicated.

* Pl. xxii. fig. 2, *Trans. Roy. Soc. Edin.*, vol. xiv., 1840.

† *Vide Quart. Jour. Micr. Sci.*, vol. viii. N.S., pl. iii., 1868.

The contraction of the auricle sends the blood into the ventricle, and the latter by the bulbus drives it into the four branchial arteries, which terminate in the dorsal aorta. The latter passes backward almost, though not quite, to the tip of the tail. Before reaching its termination (Pl. XX. fig. 1) a twig leaves the artery and goes into the lower lobe of the tail, forming, with the returning veins, an arrangement of at least four loops. Moreover, the caudal vein bends downward, producing a loop or diverticulum just where the arterial twig leaves the aorta, and receives the branches returning from the region. The four loops referred to form a fan-shaped arrangement, one loop being in front, two median, and one posterior. In its course along the under surface of the notochord, the aorta sends a twig (Owen's intercostal) upward at each myotome, and it alternates and inosculates with the veins returning to the posterior cardinal. A specimen showing these features was found so late as 1st March, and had not long emerged, so that a margin for variation must be made. The artery on passing over the urinary vesicle transmits on the left side a large trunk to the rectum (A, Pl. XXVI. fig. 2), which by and by divides, a large branch sending twigs posteriorly, while the main vessel proceeds along the superior edge, giving off branches from its ventral margin. These pass downward and join the great portal vein (Pl. XXVI. figs. 1, 2, *pv*), which slants upward on the right side of the gut to proceed to the liver. The forward current in the arterial trunk (Pl. XXVI. fig. 2) goes a little distance beyond the point marked *b* to the point indicated by *x*, where it is met by an opposing current from the artery *d*. This last current shows a distinct pulsatory movement (as in vigorous arteries). Thus, at the point of contact, there is a neutral zone which occasionally is thrown a little backward so as to impinge by jerks on the forward current. Any difficulty arising from the presence of two diverse currents in the continuous vessel is obviated by the ready exit along the comparatively large inferior twigs proceeding to the intestine. Streams of blood thus pour all over the intestine in a downward direction, and are collected by the great subintestinal (portal) vein. The vessels from the anterior artery (see Fig. 2) curve downward to the lower border of the gut, and as the intestinal vein in this region is above the lower margin of the latter, the branches going to it therefore curve upward. On reaching the liver the great intestinal (portal) vein breaks up into many branches, and from the margin of the organ large vessels pass to the posterior region of the yolk-sac (Pl. XXI. fig. 1, *yvs*), where their course has already been described. The cranial circulation is not readily made out. A large curved trunk, the hyoidean (Pl. XXI. fig. 4, *cv*), leaves the anterior branchial vessel near the fork of the jaw, forms a loop behind, and passes forward between the eyes. Its course is hidden by the pigment of the latter. These vessels are proportionally larger than in the salmon, and the same may be said of the jugulars, which are in intimate relation to the otocysts. Such variations are probably associated with the differences in the configuration of the parts in the respective species. The ventral branch resulting from the union of the hyoidean and two first efferent branchial arteries, and which supplies the

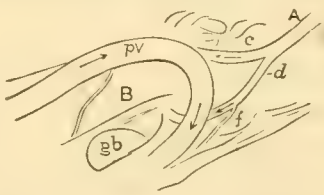


FIG. 2.—Anterior curve of the portal vein. Right side.

ventral fins of ordinary Teleosteans, is absent in the wolf-fish, which has no pelvic fins. The carotids pass along the base of the brain to the front of the snout, and the venous blood is returned by two large trunks, *vn* (jugulars), descending at the posterior border of each ear (*au*), and joining the anterior cardinals to form the ductus Cuvieri (see Fig. 3). A very distinct, though small vessel (ophthalmic), sends a swift stream of blood backward over the eye.

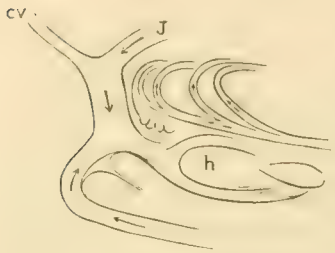


Fig. 3.—Great vessels near the heart. Right side.

If we examine the circulation at a stage two months later than the foregoing period, its complexity has considerably increased, not only in regard to the vascularity of the branchial lamellæ, but also by the great development of the vessels above and below the vertical aortic trunks. The vessels are more numerous than in the salmon one day old, and extend beyond the muscle-plates into the marginal fin dorsally and ventrally.

The action of the heart is interesting, and in an example observed on 1st April it was as follows:—The sinus is distended with blood mainly from the large vitelline vein, then the auricle fills, and its contraction distends the ventricle. The contraction of the latter, again, expands the bulbus, dilating every crevice. Sometimes, as in the salmon, the ventricle does not quite empty itself, a feature due probably to the structure of its reticulated muscular walls. In the salmon, when the chamber is distended, and just before contracting, processes of the red fluid dip into the whitish walls, and show that even at this early stage the cavity contains muscular bands and interspaces. In weak or dying specimens of the salmon the auricle contracts more sharply than the ventricle, the latter having a slower vermicular motion. The current in the large venous trunk (cardinal), just before the contraction, often gives a jerk backward, this recoil being apparently due to the valves of the auricle, and its effects are visible in the remotest part of the venous system, especially in the sac near the base of the tail. The shortening of the auricle, a most marked movement in contraction, is towards the ventricle—just as the hand would squeeze an elastic bag chiefly at its fundus in order to drive the fluid by a jerk out of the muzzle. In these young fishes this organ is the *ultimum moriens*.

In the salmon of the sixth week the aortic bulb is covered with pigment-corpuscles, apparently in the pericardial serous membrane, which elsewhere contains similar pigment. A band of muscular fibres is connected with the bulb a little way up, and the fibres are probably the same as those observed at the side of the pericardium anteriorly in *Anarrhichas*. The contractions of the heart are most favourably observed from the left side.

The heart of *Anarrhichas* in January had comparatively thin walls, which showed, in section, few fibres, but many nucleated cells. The thick region was towards the bulbus, into which two conspicuous valvular folds (aortic valves) project. In section, the area of the entire organ is cellular, with the exception, perhaps, of the external fibrous investment, the cells being apparently bound together by a protoplasmic matrix. This

condition is precisely similar to that in the young Clupeoid, $\frac{1}{4}$ inch in length, the heart being saccular, and consisting of 3 or 4 layers of cells, many of them very round and prominent. The endothelium is, however, flattened. The cells in the wolf-fish project internally, so as to occupy a considerable portion of the central area, but much less now than afterwards. The bulbus in contraction at this stage is nearly cylindrical, its central cavity being evident just above the valves, and it is on minute examination seen to be composed of fibres and cells. The auricle has a cellular wall, the cells apparently being also fibre-cells, and the wall is now better defined externally, as if from more continuous fibrillation, this differentiation of a stronger outer layer being also observed in the young Clupeoid at the stage just referred to.

As the organ attains greater complexity, the ventricle largely assumes a reticulated appearance from the vascular ramifications of its walls (Pl. XXV. fig. 1, *ven*), the whole being in many sections not unlike a fibrous sponge—a condition characteristic of the heart in the adult. This structure is also shown in the young Clupeoid, when $\frac{7}{24}$ inch long—small spaces being formed in the loose saccular walls, which, as in the slightly younger stage, are studded with large scattered nuclei. Quite different is the structure of the ventricular walls of the post-larval goby, $\frac{5}{24}$ inch long, the spaces being formed in very dense and thick tissue. The walls of the auricle in *Anarrhichas*, as in *Clupea*, *Gobius*, and others when $\frac{1}{4}$ inch long, consist of a thin muscular layer lined by endothelium. In the most advanced stage of the wolf-fish (20th June) the two valves at the base of the bulbus are well defined. The reticulations of the conical ventricle are much finer and more numerous, and the fibres more distinct. With the exception of the central chamber, which occupies about a fourth of the thickness towards the base, the whole organ is reticulated in this manner, and the blood passes into the reticulations. So accurately do the auriculo-ventricular valves close that in the preparation a thick column of blood projects into the auricle, the mass being covered by a tense membranous layer, apparently valvular.

The heart in the young salmon, at thirteen and forty-five days respectively, presents corresponding features to that of the wolf-fish, though the nuclei in the muscle-cells are much more distinct both in the early and later stages.

When fully developed the circulation in the larval wolf-fish presents, in regard to the vertical or what may be called the vertebral branches of the aorta, a similar arrangement to that in the salmon, which has about 26 or 27 of them. These somewhat differ in the latter fish in the several parts of the body. Thus the anterior branches (Pl. XXVIII. fig. 2, *a*) course straight up from the aorta to the middle of the trunk, then give off the oblique twigs (*b*) which proceed downward and backward so as to form the oblique lines so noticeable in the living fish. They alternate with venous trunks (*c* and *d*) having the same direction. These arterial twigs admit only a single line of corpuscles, which proceed with great rapidity, and join the respective veins (*c*), and then by the larger trunk (*d*) debouch into the cardinal. Beyond the oblique arterial branches just noted the vessels course upward and slightly backward to the border of the muscle-plates, and give off various twigs before terminating in the venous radicles. Posteriorly the oblique branches appear to

be less complex, and finally they form simple twigs towards the termination of the chorda. The arterial branches along the sides of the body appear (in optical section) to be more deeply situated than the veins.

At this time no blood-vessel extends beyond the line of the muscle-plates—including those of the tail; indeed, it is not till the third day that three or four loops of capillaries (Pl. XXVIII. fig. 3, *ax*) pass from the distal ends of the vertical vessels in the region of the adipose fin. They increase in number about the tenth day, yet at this period none occur in any other fin, except the tail. This is a noteworthy feature, though it is in consonance with what Alex. Agassiz has generally observed, viz., that the posterior dorsal is the first to be differentiated.*

In the wolf-fish the anterior region of the intestine (Pl. XXVI. fig. 2) is supplied by a large artery (mesenteric) *d*, which leaves the aorta on the right side, proceeds towards the intestine, and bifurcates after a short course. The superior branch runs along the posterior third of the upper part of the gut to inosculate with the main artery from the posterior end, as formerly mentioned. The other trunk passes to the lower side of the gut, and gives twigs anteriorly as previously seen, and these terminate in veins passing upward to the intestinal (portal) vein. A hepatic branch is also sent to the liver. Another branch (the subclavian) is given off by the aorta in front to each pectoral. In the salmon, again, besides this branch, the aorta sends twigs to the right and left sides of the yolk-sac. These, however, were not noticed in *Anarrhichas*, though they may have been present. When about a week old, moreover, minute branches occurred in the salmon in the space between the yolk-sac and the ventral fin. Some of these seem to come from the arterial twigs of the sac, others from the oblique twigs on the side of the body. In the newest and most minute capillaries in the developing fish (salmon) the blood-discs pass edgewise, and at intervals, the rest being simply a flow of pale fluid: nothing else at least could be observed.

Caudal Circulation.—The circulation in the tail of *Anarrhichas*, at the stage shown in Pl. XXVII. fig. 2, may very well be contrasted as regards the arrangement of the vessels with that in the salmon two or three days old (Pl. XXVIII. fig. 1), though it has to be borne in mind that the presence of the fairly formed cartilaginous hypural elements in *Anarrhichas* has an influence on the relations of the parts. The aorta (*ao*) in the wolf-fish leaves the notochord just at its dorsal bend, a twig passing up, over the chorda, a little beyond the point of departure. The course of the vessel is backward and downward between the upper and lower hypurals. The next branch is a slender twig (*cad*) which passes, with a nearly equal interval on each side at its origin, almost to the tip of the notochord, where a few coils occur. It then enters the venous system. It is, probably, the representative of the small artery which, about a fortnight before, went upwards along the notochord and returned by a similar vein, as in the salmon.

At the posterior termination of the hypural fissure the artery splits—a branch proceeding dorsally and another ventrally—the two lying nearly in a continuous line. From these a series of more or less parallel loops pass outward and obliquely downward

* *Proc. Amer. Acad. Arts and Sci.*, vols. xiii. and xvii.

in a fan-like manner into the caudal expansion, the whole having a somewhat semicircular outline, since the dorsal and ventral branches are less prominent than the median. A considerable margin of the tail is devoid of vessels. A downward loop is usually formed by the vessels just described, which enter the vein, and various inosculations also occur terminally. The terminal, dorsal, and ventral series present slight irregularities, the dorsal loops especially being broader and less definite. The venous twigs from the arteries just alluded to pass forward in a similar direction to the two large venous trunks running along the posterior border of the hypurals. In regard to the axis of the body, these veins, as well as arteries, lie at an angle of about 45°, the ventral edge, moreover, having twigs which curve even further forward. By the union of the foregoing venous ramifications, the great caudal is formed. It lies beneath the aorta, and follows the same curved course as the artery.

The circulation in the tail of the wolf-fish exhibits, at this advanced stage, a complexity similar to that in the salmon two or three days old, and the contrast between their rate of development is thus very great (*conf.* Pl. XX. fig. 1, wolf-fish newly hatched, with Pl. XXVIII. fig. 1, salmon newly hatched). It is unlikely that the development of the former in the egg is much more rapid than that of the latter, yet the wolf-fish on being hatched presents only a few loops of vessels below the straight notochord, while the salmon has attained a complexity of organisation in regard to the vessels and the curvature of the notochord only reached by the former two months later. Moreover, the nearly horizontal direction of the median vascular loops in the salmon is in contrast to the obliquely downward direction of those in the wolf-fish. It must, however, be remembered that the influence of altered circumstances (*e.g.*, those in the Laboratory) upon the eggs of *Anarrhichas* is unknown: yet other eggs with thick capsules do not seem very readily affected by such external conditions.

The size of the arterial trunks in the tail of the salmon seems to be smaller in comparison with the veins than in the wolf-fish, and, moreover, the former has a large venous sac (comparable to the caudal heart of the eel) at the upward bend of the notochord, forming a large ovoid dilatation sloped upward and backward, and with a siphonal bend dorsally, and a slight contraction ventrally (Pl. XXVIII. fig. 1, *cvs*). No pulsation is ever present in it, except the impetus from the pulsations of the arteries and from the action of the auricle. Stasis very readily affects this sac. In the somewhat older larva as much blood passes by the vessels beneath as through the sac in these circumstances. The sac seems to diminish rapidly, for it is indistinct on the thirteenth day, though the increased amount of pigment renders accurate observation difficult. When about a week old, a secondary enlargement in the form of a rounded sac sometimes occurs just behind the former.

In the more advanced condition, as at the end of March, the vessels in the tail of *Anarrhichas* (Pl. XXII. fig. 2) have become much more elongated, and more definitely arranged. Further, instead of the obliquely downward direction of the main vessels, the whole form a fan-shaped arrangement, the median being horizontal, as in the salmon on the first day.

The two main branches which respectively leave the aorta and join the caudal vein

have now assumed a nearly vertical position, instead of being directed from above downward and forward. This position is due to the changes in the upward bend of the notochord, and the relations of the hypural elements. The regularity of the vascular loops towards the tip of the tail is noteworthy, each corresponding with a prominent cutaneous frill or process of the marginal (caudal) fin.

Pigment.—On emerging from the egg, about the beginning of February, the larval *Anarrhichas* shows finely stellate black pigment on the head and other parts, especially along the dorsal region of the pronephros and alimentary canal, and behind the pectoral fins (Pl. XXI. fig. 1); a considerable number also occur on the adjoining region of the yolk-sac. It so rapidly increases that a conspicuous blackish band soon stretches from the pectoral fins to the anus. The pigment just described as passing along the dorsal line of the alimentary canal is found in section to be deeply seated, and to be scattered near the commencement of the segmental duct—on each side of the aorta and below the notochord. The pigment dips between the involutions of the duct anteriorly, and afterwards forms a lining to the roof of the perivisceral cavity, splitting in the centre to enfold the segmental ducts. It continues all the way back to the urinary vesicle, diminishing much posteriorly, then dips in between the vesicle and the rectum and ceases. In the case of those embryos long retained in the egg, the pigment is abundant. The general hue of the fish is a translucent straw-colour, with the exception of the blackish pigment just referred to. As the latter increases it is found that dorsally, in lateral view, it becomes aggregated largely in two lines above the level of the notochord, and gradually reaches the base of the tail. Much of this pigment is doubtless deep seated, that is, is developed in the membranes of the brain and spinal cord.

In the beginning of April the blackish dorsal and ventral bands on the side become conspicuous. Each commences behind the pectoral fin, and envelops the lateral region of the body almost to the lower border of the liver, where it is defined by a straight line which commences somewhat above the notochord in front, and dips slightly in its course until it reaches the anus. It covers the entire alimentary tract, and posteriorly shows numerous dorsal digitations. The head is now so closely covered by the stellate pigment-spots that it assumes a dull slate-colour, and the same hue characterises the anterior region of the body. A double line of pigment runs internally (1) along the tips of the neural spines, processes interdigitating with them, and continuing very distinctly almost to the end of the notochord; (2) the other passes from a point a little behind the head on the surface of the muscle-masses, to cease a little before the other band just described. This outer pigment-layer is within the bases of the spines (interspinous bones). Towards the end of the month a still further increase takes place in the pigment between the snout and the base of the tail, and it extends latterly to the ventral marginal fin. The densest region is at the dorsal margin of the abdomen on each side, and stretching from the pectorals to the anus. The fish laterally shows a silvery lustre (from the peritoneum), with black touches, which form an obliquely striped arrangement (Pl. XXVII. fig. 1). Toward the upper region of the abdomen the colour progressively increases, so that about

the 1st of May the upper arch of the cranial cavity, and a considerable portion of the sides superiorly, are covered with continuous pigment. It extends along the spinal cord—enveloping two-thirds of its surface dorsally—while the lower aspect is free from it. The abdominal cavity has a continuous coating on its silvery peritoneal surface, and the same occurs, as previously noted, round the segmental organs. A dense layer of pigment also lies beneath the skin, over the muscles, and posteriorly the upper arch splits to send off a layer to the tip of the interspinous bones. The latter layer ceases a little above the bases of the V-shaped fin-rays. There is considerable variation in the pigment, some specimens towards the end of June, with the yolk-mass completely absorbed, presenting in transverse section, besides the continuous layers, large isolated pigment-masses here and there, breaking the continuity of the layer, both in the subcutaneous and peri-nervous regions.

The silvery sheen extends a short distance over the yolk-sac. The dorsum of the head is deeply pigmented, while the sides are less so. A little below, the lobes of the brain are outlined by their blackish pigment. About the middle of May, the condition of the young fish is shown in the figure before mentioned (Pl. XXVII. fig. 1). The pigment on the dorsum and sides is dull blackish or a uniform dull grey, with black specks. The abdomen is silvery and iridescent, as well as dotted with black pigment-corpuscles. The pectorals have a little pigment at their bases, and the same is present along the bases of both dorsal and ventral marginal fins, the former being definitely banded. The tail is still translucent. The iris is iridescent silvery, with black pigment—chiefly visible superiorly.

When about five inches in length, the dorsal fin has about a dozen black spots at intervals, the anterior being nearer the free edge than the posterior. The sides are also marked by a somewhat reticulated arrangement of spots which, in a few instances, coalesce to form bars. The lateral dark patches proceed from those in the dorsal fin, and meet when about a third of the body is traversed, and then they form a single or double band to the ventral border, which is devoid of them. The increase in the pigment, *e.g.*, at six inches, demonstrates how, from the former arrangement, the bold stripes on the sides and dorsal fin of the adult are formed. The hue of the latter must render it very much in harmony with its surroundings on rough hard ground amidst stones and zoophytes.

In the young salmon we find many points of contrast at this stage. The pigment on the head is much developed on extrusion from the egg. A few black pigment-corpuscles occur beneath the cranial tract and along the spinal cord, but they are isolated, and often in the abdominal roof only a single one occurs in a transverse section of the fish. In this region, also, a line of pigment passes dorsally on each side of the median (embryonic) fin. A few, again, occur at the base of the ventral median fin. Both cease before reaching the tail. The young salmon at this period is of a translucent pale yellowish hue, with a tinge of pink, while a considerable number of pigment-corpuscles are present on the head, and a chain of them along the neurochord. The large oil-globule is of a dark orange-colour. The pigment very soon becomes denser at the upper part of the yolk-sac, as well as over the body of the fish. The indications of the "parr-marks" occur at the third week. A little later (fourth or fifth week) the pigment

is much increased, especially at first over the opercular region, and other parts of the head. The "parr-marks" on the sides are eleven in number, though, from the close proximity of several, they do not appear to be so numerous. They are not symmetrical on the sides, the fourth being double on the left side, whereas it is the third that is so on the right in the specimen examined. Along the dorsum the pigment is arranged in a double chain, while the head shows an hour-glass pattern. The black spot on the operculum is well marked. The tail laterally and posteriorly exhibits a brownish-pink hue from the presence of the reddish pigment-corpuscles. These latter are likewise distributed on the general surface of the body and on the dorsal fin.

About a fortnight later the entire body is covered with pigment-corpuscles, which are larger and more closely aggregated at the "parr-marks." Minute glistening granular bodies also occur in various parts of the integument. The dorsum anteriorly has a considerable member of pinkish-red corpuscles, giving it a reddish tint to the naked eye. Small corpuscles of the same hue occur in the "fatty" fin, in which the vessels ramify very plainly.

Along the dorsum (behind the pectorals) are seven pigment-masses. The first, immediately behind the pectorals, is large and distinct. The second, also distinct, is situated at the anterior part of the dorsal fin, covering a space in front and a portion on each side of the fin. The third has similar relations to the posterior part of the fin, besides proceeding some distance behind it. An elongated and less defined mass follows, in front of the "fatty" fin, and connected with a smaller patch at the anterior border of the fin, which proceeds a short distance on either side. Eight fairly definite lateral bars are present on the left side, with a less evident ninth bar at the tail. On the right, likewise are nine, the sixth being placed a little behind the (posterior) margin of the dorsal fin, and so elongated and large as to appear double or compound. The ventral surface is silvery white, and the general colour of the back greenish. Scales are now present on the dorsum, and mucus scraped from the surface is found to contain many flat nucleated cells (epithelium) of a delicate transparent character, with a large granular nucleus, and one or more nucleoli.

The young salmon, about a month older, shows a little variation in the "parr-marks." Thus, in some eleven occur on the left, while nine are present on the right side. The dorsal pigment remains much the same as above described. A reddish tint is still observable at the margin of the fins. The young fishes, however, differ somewhat in size and colour, some being quite light, others very dark under the same conditions. In many examples a large yellowish patch occurs in the posterior part of the cranial region, while in front is a greenish-yellow area. The usual changes in tint, however, are observed on removal from a darker to a lighter situation, except in sickly or apparently dying fishes. The round glistening bodies composed of transparent granules are still abundant.

The pigment of the two species mainly considered in the preceding pages offers a few interesting features to which brief reference must now be made.

The young wolf-fish is uniformly tinted, or at least exhibits no bars, in the stages up to

the length of $1\frac{1}{8}$ inch; whereas the adult wolf-fish is boldly barred with dark pigment. On the other hand, the young of the salmon, as well as of allied species, are just as prominently barred in their larval state, as they are uniformly tinted in their adult condition. We have seen that the young cod is at first boldly speckled, and later is definitely tesselated, whereas in its adult state the tints are more or less uniformly arranged.

The ling (*Molva vulgaris*), again, after the ochre-yellow colour of the early embryo—a colour which extends along the enormous pelvic fins of the subsequent stage—becomes, in a more advanced condition, beautifully striped, and still later is barred in a most striking manner, while the adult form is almost as uniformly tinted as the cod. The young green cod (*Gadus virens*) is, however, uniformly tinted both in its young and adult condition, the larval stage not yet having been described; and, as far as is known, the haddock and whiting (Pl. XVII. fig. 12), after the absorption of the yolk, do not exhibit any divergent feature in regard to colour. On the other hand, the young gurnard (*T. gurnardus*) shows little that is noteworthy in the pigment of the early stages, but when $\frac{3}{4}$ inch in length it is characterised by the remarkable crescentic disposition of the pigment on the pectoral fins. The dragonet (*Callionymus*) is less beautifully tinted in the young stages than in the adult, but it is noteworthy that the ventral surface of the abdomen is blackish in the post-larval stage—white in the adult.

The rocklings (*Motella*) are distinguished by their remarkably long ventral fins, the base being white and the tips black. In the *Pleuronectidæ* there is a tendency to transverse rows of blackish spots, as in the turbot (*Rhombus maximus*), or in an earlier stage to dots along the bases of the marginal fins, both dorsal and ventral.

The Integument.—Few features of interest are found in the integument of other post-larval forms, as the scales appear to be late in developing, and the various dermal and epidermal strata are not readily distinguished. In some forms, as in *Callionymus*, $\frac{1}{3}$ inch long, and *Cyclopterus*, large cellular spaces occur from the snout to the tail—developed probably in the Malpighian stratum of the integument, and by their increase in size they are pushed towards the surface. Their contents are usually clear in stained sections; but in *Cyclopterus* they are coloured very deeply by Beale's carmine, and in all cases are probably glandular. In *Cottus*, $\frac{3}{8}$ inch, also very large spherical cells of a similar character appear; and in the post-larval *Labrus*, $\frac{7}{16}$ inch in length, they are most numerous over the frontal and epiotic regions.

Serous Spaces.—In the early larval condition of certain forms considerable serous spaces occur in the dorsal regions of the head and trunk, but they gradually diminish, and lymphatic fluid appears to collect in chambers, often of large capacity, which occur as in the post-larval gurnard when $\frac{5}{12}$ inch in length, between the roof of the mouth and the cranial floor. A blade-like plate of hyaline tissue is developed in the membrane arching over the two supra-oral cavities. Each plate is placed at an angle, and abuts on the posterior median process of the rostrum. Again, in the cod, $\frac{11}{24}$ inch in length, a large lymphatic chamber occurs behind the urinary bladder, and a network of connective tissue occupies the contained space. Around the fore-part of the membranous cranium

in *Pleuronectes flesus*, $\frac{5}{12}$ inch in length, a space occurs—evidently filled by gelatinous or lymphatic matter with widely separated nuclei.

Pectoral Fins.—In the larvæ of the wolf-fish hatched at the time the eggs were obtained (viz., January) the movements of the pectoral fins (Pl. XX. fig. 5) were as active as those in the salmon on its escape from the ovum. Their motion within the egg, however, was not noticed at this period. As the season advanced these organs showed more vigorous motions, and were kept in rapid vibration when swimming. On the 1st of April they presented a crenate margin, and before the end of that month attained great development as large fan-shaped expansions, but during the stages under observation their axes remained more or less vertical, as indeed they are in the adult. A comparison with the salmon is interesting, since, in the wolf-fish, the pectorals remain very large throughout life, whereas in the adult salmon they are of moderate dimensions. Viewed laterally in the newly-hatched salmon (Pl. XXII. fig. 4) they are very prominent, rising above the line of the dorsum and its median marginal fin. In vertical transverse section their tips far exceed the dorsum, and thus they present a great contrast to those of the wolf-fish, which do not at this stage reach so high. Their plane is nearly parallel with that of the body, and they are more or less rounded in form. On the fifteenth day they show embryonic fin-rays, and distinctly droop to the sides, and do not extend so much above the dorsum (Pl. XXII. fig. 8). As development proceeds, they gradually increase in size, and by the rotation of their axes they, in the fourth or fifth week, assume a horizontal position (Pl. XXII. fig. 10). They form, indeed, two shark-like organs which, when the fishes are resting on the stones at the bottom, are often moved in a reptant fashion, after the manner of Chelonian fore-feet. Moreover, the fin of the parr, at a somewhat later stage, becomes less rounded (more lanceolate) than in the earlier form. In horizontal sections of post-larval Gadoids, $\frac{1}{2}\frac{1}{4}$ inch long, the free fin-plate of cartilage is separated by an interval from a proximal (coraco-scapular) plate, internal to which is the hyaline clavicular rod. The interval referred to is filled up by deeply stained cellular tissue which forms a thick protruding band.

Ventral Fins.—A similar change takes place in the shape of the ventral fins in the salmon, from the rounded form of the seventh day salmon (Pl. XXVIII. fig. 2) to the lanceolate outline of the adult. These organs (ventral fins) are sometimes used for support when resting on the bottom. In the early larva only the embryonic fin-rays are present, but at the end of the third or fourth week there is externally a pale margin, with few cells, which increase from without inward until a mass of cells—traversed by the fin-rays—appears.

The ventral fins in marine fishes develop late in larval life, one of the most rudimentary stages occurring in a post-larval *Ammodytes* (?), $\frac{1}{4}$ inch in length. On the flattened ventral surface two angular knobs appear laterally below the posterior hepatic region. In transverse section the epidermic evagination exhibits an inner columnar layer, with a dense central core, limited internally by the thin peritoneum. A similar appearance is presented by the ventral fin-buds in *Gastrosteus spinachia* at a late larval stage. In *Pleuronectes flesus*, $\frac{9}{2\,4}$ inch in length, the buds are more advanced and have the form of

ventrally directed flaps on each side of the diminishing median embryonic fin-membrane. In the central core above referred to, a simple bar of cartilage passes downward from a point immediately below the peritoneum, at the anterior border of the liver, and ends, near the tapering margin of the fin-bud, in a dense aggregation of small cells deeply stained in the preparation. In a Gadoid, $\frac{3}{4}$ inch in length, similar cartilaginous plates appear, not, however, in bold projecting flaps of the integument, but in flattened horizontal ridges; this difference in position being due, no doubt, to the flatter and more obtuse character of the ventral surface in the post-larval Gadoid. Posterior to the paired cartilaginous plates, which have an upper and a lower muscular mass, an expansion of the integument forms a membranous fin supported by four or more hyaline rays. The fin-rays at this time consist of paired hyaline rods, semilunar in transverse section, each pair enclosing a strand of dermal tissue. A still later stage is seen in the post-larval goby, $\frac{7}{24}$ inch long, in which the two basal skeletal rods of the developing ventral fins approximate, and are united posteriorly, forming an angle, with the apex directed backward. Thus early is the union of the ventral fins effected which results in the disk-like structure characteristic of the adult. The liver lies immediately over the developing ventral fins, which are slightly anterior to the position they subsequently occupy.

Median Unpaired Fins.—In the larval wolf-fish the marginal fin-membrane commences behind the head in a position similar to that in the salmon, and extends all round to the anus, and again forward in front of it to the yolk-sac. Proportionally it is much less developed than in the salmon, and while the changes in its outline in the latter are complex, those in the wolf-fish are less so. Moreover, whereas the marginal portion of the tail of the salmon does not increase much at the period of absorption of the embryonic fin, the contrary is the case in the wolf-fish, whose caudal expansion attains large dimensions as the fin of the body diminishes. Whether this is altogether due to the increase of the marginal web of the tail, or absorption in the other parts, is doubtful. Probably both causes are concerned. The embryonic fin-rays appear first in the caudal region, and afterwards in the anterior region. As the larval fish increases in size, the marginal fin remains stationary, its further apparent diminution being due merely to the general increase in the bulk of the body. It, however, increases in thickness, and spinous rays are developed during the second month. On completing the larval phase, *i.e.*, on the absorption of the yolk in the beginning of June, the number of dorsal spines is seventy-one; the first pair are separate, and the second diverge at the tip, while the last is single and small. The ventral spines are forty-four in number, and the last likewise is single and small.

In the salmon the marginal fin (Pl. XXII. fig. 4) shows, on emergence, considerable differentiation. Thus the first dorsal is well marked, though it has only the granular structure characteristic of the rest of the fin. The adipose fin is indicated by the eminence situated between the former and the caudal, which is somewhat lobate, and generally shows a slight notch above the tip of the notochord, marking, apparently, the homologue of the embryonic tail-fin. The anal is distinguished by an elevation posterior to the anus,

and a similar prominence (pre-anal) corresponding to no structure in the adult fish, and not comparable to the first anal of the Gadidæ, occurs between the ventral and the anus.* When a week old, these portions, which correspond to the regions of the permanent fins, are denser, the other parts being very thin, and apparently undergoing absorption. The embryonic rays are now distinct. Meanwhile the blood-vessels begin to ramify in the "fatty" fin (Pl. XXVIII. fig. 3), and the capillaries in front and behind the primary series are on the ninth day increased; they soon, indeed, extend throughout the entire length of the fin. Several indications of true fin-rays occur in the first dorsal, and at the end of a fortnight the embryonic marginal fin has, to the naked eye, nearly disappeared, so that the permanent fins are more boldly marked. Pigment appears in both dorsal fins at the same period; while pale capillaries ramify in the anal fin, and stretch nearly to the tip. They probably also develop in the dorsal and ventral; but they were not seen. The marginal (embryonic) fin is now almost absorbed, except in the interval between the ventral fin and the anus.

Between the fourth and fifth weeks, the dorsal and anal fins show the cartilaginous rays, while the membranous parts between them are widened and coloured by numerous yellow and brownish pigment-corpuscles. Thirteen rays occur in the dorsal, and the same number in the anal fin, and the interspinous elements produce wavy marks beyond the muscle-plates. Both fins have crenate borders, as in the tail at this period; while the adipose fin presents a fibrillated aspect, and has a network of fine blood-vessels. All the fins are proportionally larger than in the adult, as observed in the outline of an average specimen (Pl. XXII. figs. 10 and 11). In minute structure the dorsal and other fins already present most of the characters of the adult. Thus, at the anterior part of the dorsal, are two narrower and shorter rays, the first a simple spike, the second consisting of two which form a loop. At the base of the larger rays is a projecting median point, and the terminal process is long, and almost unciform. The pigment is chiefly placed on the cartilaginous rays.

In considering the condition of the median fin-rays of these young fishes, it will be observed that on the thirteenth or fourteenth day the dorsal of the soft-rayed salmon corresponds nearly with the condition in the adult, but in the anal fin the number of rays on the tenth or the twelfth day, viz., thirteen, is in excess of the number in the adult. In this respect, however, it is doubtful how far authors in numbering the rays have anatomically examined the parts, or how much they have depended on external appearances. On the other hand, the osseous rays in the dorsal of the young wolf-fish seem, if DAY be right, to be fewer than in the adult, viz., 71 as compared with 72 or 74 (DAY), while the rays in the anal present a similar condition, viz., 44 in the young as against 45 to 46 in the adult. An examination, however, of the skeleton of a fine adult in the University Museum here shows that the number of the dorsal fin-rays exactly corresponds with that of the young forms just mentioned, and so with the ventral. There may be variation;

* The outlines of the fins of the young salmon seem to differ considerably from those of the larval Lochleven trout, as shown by Mr J. T. CUNNINGHAM, *Trans. Roy. Soc. Edin.*, vol. xxxiii. pl. i. fig. 4.

but it is remarkable that so little exists. Mr Day * had, therefore, certain grounds for stating that fin-rays do not materially increase with age.

The condition of the growing rays and of the interspinous elements in certain other post-larval Teleosteans is interesting. Thus, in a section of the caudal trunk of a gurnard, $\frac{5}{12}$ inch long, four series of interspinous cartilages are developed in the connective-tissue strand which extends upwards from the neural arch. The neural spine is the proximal element, and has the form of a rounded nodule clothed on each side by a plate of hard hyaline tissue. The third nodule in the series is large and irregular, and like the second presents a cartilaginous structure only; but the highest nodule, lying at the base of the 2nd dorsal fin, exhibits on each side a horizontal hyaline plate passing outwards parallel to the plane of the flattened dorsum. The fin-rays are paired rods of hyaline tissue, and at this time each rod is separated from its fellow by intervening tissue. Each of the cartilaginous elements just described has its special muscular strand on each side, and it is possible that they may at a later stage unite to form one javelin-like neural spine. Further forward, indeed, the neural spine does develop as a single rod of cartilage surmounted by a nodule of the same tissue which is trifid superiorly. In *Cottus quadricornis* the neural spine in the mid-trunk region is cartilaginous, with one superior (interspinous) element; but the neural arch itself is formed by two dense hyaline arms which grow out from the perichordal ring of the same tissue. In the post-larval goby (*Gobius ruthensparri*) the interspinous element appears before any neural arch or spine is developed, and it has the form of a rounded nodule at the summit of the connective-tissue continuous with the perichordal sheath. In the young wrasse, $\frac{7}{16}$ inch in length, no supra-neural cartilage appears at all in the region of the dorsal fins. The fin-rays are, as usual, formed by the union of paired hyaline rods, having a semilunar form in transverse section—the concave surfaces being opposed, and the neural spine, as will be described later, is formed of hyaline matter.

On escaping from the egg the tail of *Anarrhichas* is more or less lobulated, though in many it is lanceolate. A distinct constriction (Pl. XX. fig. 1) occurs in front of the organ, which then gradually widens out—the dilatation being more marked inferiorly than superiorly. The notochord goes straight backward from the nuchal curve to the commencement of the caudal region proper, and then tapers to the termination, the axis of this part being in the same line as that in front, viz., horizontal. In many views, in newly hatched forms (January), a slight fold appears at the margin of the caudal fin, in a line continuous with the notochord; but whether this is a definite structure or not is uncertain. All that can be said is that the appearances indicated in the figure (Pl. XX. fig. 1) were frequent, and recalled the notch above the tip of the notochord so familiar in the larval salmon. Structurally the tail, at this stage, presents a minutely cellulo-granular appearance (due to the cutaneous elements), most marked in the thicker central region, and becoming translucent towards the margin. The embryonic fin-rays,

* [It is with deep regret that the authors have just received intimation of the death of this experienced and meritorious worker in the field of Ichthyology—both British and foreign.]

like fine fibres, radiate over the whole area of the organ. The notochord transfixes the tail considerably above the median line, leaving a much larger proportion of the lobe beneath than above, and into this the blood-vessels pass. A little posterior to the marked caudal diminution of the notochord the neurochord abruptly narrows, and a delicate continuation (Pl. XX. figs. 1 and 3) proceeds to the tip of the former.

In the course of the succeeding month (February) the dorsal bend of the notochord commences, so that on the 17th a considerable change in outline has occurred. The upper border, especially along the posterior line, becomes prominent, while the inferior is less so, and the hind edge assumes a broad blunt outline (Pl. XX. fig. 3). It is evident that the inferior lobe of the tail in the early stage (Pl. XX. fig. 1) now becomes more or less the posterior, a change, perhaps, partly due to the terminal and upward curve of the notochord. The latter at this stage is much less marked than in the salmon of the first day. The appearance of the hypural elements (Pl. XXVII. fig. 2), as already indicated, probably aids in the transformation. The notochord is still less curved than in the salmon of the first day, and the posterior hypural margin slopes downward and forward. The hypural (cartilaginous) element most anterior (*huc*) is quadrate, and devoid of the notch seen by Professor Huxley in that of *Gastrosteus.** Its longest side is directed inferiorly and posteriorly. The posterior or superior hypural cartilage is triangular in outline, its longest side being applied to the under surface of the ascending notochord, which projects about half the length of this side beyond it. The bases of five or six caudal rays rest on the larger hypural, and a somewhat smaller number on the upper. They may be estimated at twelve in the earlier stage (March). In the following month (April) the further curvature of the notochord upward is accompanied by a tilting of the posterior edges of the hypurals into a nearly vertical position, and the greatly elongated vessels now run straight outwards along the rays. The posterior margin of the caudal fin has also become conspicuously crenate, and at this stage (Pl. XXII. fig. 2) the inferior margin is more rounded than the superior, which ends after a straight course somewhat abruptly in a crenation. In front of the tail, ventrally, a slight inflection of the marginal fin occurs. The notochordal sheath now shows serial constrictions indicating the separation of the centra.

In the next stage (Pl. XXVII. fig. 3) the tail is considerably elongated, and its vertical diameter is diminished. The notochord is less in proportion to the other parts, while the anterior, or inferior, hypural has increased in length, and shows a distinct upward curvature at the base.

There are upwards of twenty caudal rays, *i.e.*, about twenty-four, a larger number than is present in the adult. Day records the number in the adult at fifteen to eighteen, while in the St Andrews University Museum three specimens each possess twenty-one.

The fin-rays show three vertical rows of articulations, and they spread out distally, and terminate in fine fibres, like those of the embryonic fin. The marginal crenations, posteriorly, are now so disposed that they correspond with the expanded ends just

* *Quart. Jour. Micr. Soc.*, 1859, p. 40, pl. iii. fig. 1.

mentioned. A further stage is shown in the coloured figure of the young fish about the middle of May (Pl. XXVII. fig. 1). In this the upward direction of the dorsal border of the tail is evident, but the organ is perhaps less elongated (antero-posteriorly) than in the previous stage.

The difference between the tail of the larval fish and that of the adult is obvious, for in the latter it is somewhat dwarfed by the great development of the median fins—dorsal and ventral—and its antero-posterior diameter is considerably less than the depth, for instance, of the dorsal; whereas, in the young stage, its long diameter much exceeds the depth of the latter, and both the dorsal and the ventral diminish in front of it so much that it is very prominent. Probably the condition of the tail has relation to the more active pelagic habits of the larval animal at this period.

The development of the caudal region in the salmon was observed at the fortieth day after fertilisation. The tip at this stage is very transparent. The termination of the notochord is gently curved upward and ends in a somewhat blunt point, a short distance within the free border, the cells ceasing before the tip is reached. The notochordal sheath is well marked. Above the notochord the neurochord is about the same breadth. The embryonic fin-rays stretch outward as in the marine Teleosteans. Thus the embryo has reached at this time a more advanced condition in regard to the notochord than the larval wolf-fish in the early months.

In the newly hatched salmon, again, the tail (Pl. XXVIII. fig. 1) has attained a degree of development comparable with that of the wolf-fish at the stage shown in Pl. XXVII. fig. 2, for the true fin-rays have made their appearance in addition to the transient embryonic rays, though the great increase in cellulo-granular tissue obscures both. On the tenth day the fin-rays number about twenty, and they abut on the hypural cartilages. They are split a short distance from their origin, and blend, in ordinary views, in the embryonic fibres at the tip and the cellular stroma of the organ.

The hypural elements have also increased considerably, and show a cartilaginous structure, forming a clear space behind the notochord. The notch remains in the margin beyond the tip of the chorda, indicating perhaps the dorsal and ventral lobes; but the tail is narrower, and the posterior margin is less curved.

When a fortnight old, lines of pigment occur in the tail, along the fin-rays, leaving clear intermediate spaces. The arteries run along the latter, and the veins return by the dark lines. There is now no notch superiorly to indicate the tip of the notochord, and the free margin is somewhat undulated. The upper border of the tail is more prominent than the corresponding lower margin, just as we see in *Anarrhichas*. The segmentation of the fin-rays produces wavy lines in the tail. Already the curved portion of the notochord is diminishing in proportion to the rest of the tail, and is now much obscured by pigment. Between the fourth and fifth weeks the articulations of the cartilaginous caudal rays produce three wavy vertical lines, with their convexity directed backward. The rays are also more distinct, and for the greater part of their length are free from pigment, the base alone possessing it. The posterior margin is uneven—from crenations,

which correspond to the fin-rays. Numerous brown pigment-corpuscles exist in the intervening membrane. From the curved portion of the notochord the hypurals (about six in number) project backward, besides an opaque mass at the tip of the organ, which may be a rudiment of one, though no cartilage-cells can be made out. The fourth ray is much broader than the others, and has the form of a long bent spatula. On comparing the salmon of this period with LEREBOULLET's trout at a similar stage,* the following differences appear:—The fifth hypural from the tip is large and broad in the trout, instead of the fourth. The fin-rays in the trout are fibrillar throughout, and have no articulations; whereas in the salmon they are only fibrillar along the terminal third, and have the articulations described above. The development of the trout must therefore be slower, though in LEREBOULLET's figure the hypurals are well formed; or perhaps the figure itself is deficient. The condition of the tip of the notochord would seem to show that the stage figured is really earlier.

The pigment in the tail subsequently increases, as also do the fin-rays, which at this stage amount to twenty-three or twenty-four; whereas DAY gives those of the adult at nineteen. Four vertical lines indicate the articulations of the rays—the first or anterior being most curved.

The caudal region just described, and that of the wolf-fish, offer several interesting points of contrast, the most noteworthy of which is, perhaps, the great complexity of the circulation in the former on hatching, and the conspicuous curvature of the end of the notochord. Besides, the divergent condition of the hypural elements is striking, the salmon having five or six narrow elongated hypurals along the upward flexure, while the wolf-fish shows only the two broad plates, as in *Gastrosteus*.† It is probable that this diminution of the hypurals coincides with a reduction in the number of vertebræ in the curved portion of the notochord, a supposition borne out by appearances in the salmon —for indications of six or seven constrictions are visible in that species in the region of the hypurals, that is below the atrophied terminal process, which is lodged between the fin-rays. On the other hand, only two are seen in the wolf-fish, and though not shown by HUXLEY in his figure of the stickleback, similar features were probably present. The salmon, at any rate, would thus appear to be more heterocercal than the wolf-fish.

Notochord.—The notochord in the newly hatched *Anarrhichas* (in January) is similar externally to that of the salmon—that is, it has the usual pointed anterior end, with the downward curvature toward the œsophagus. The structure of the chorda also corresponds, though on the whole in the wolf-fish it seems more firm, since it preserves its circular outline (in section), and its cells appear to be smaller. The notochord of the salmon is prone to collapse, a feature, however, that may be due to the preparations. Posteriorly, again, a decided difference exists, since the notochord in the wolf-fish is at this stage quite straight. The straight notochord of the young Clupeoid, $\frac{5}{24}$ inch in length, is remarkable for the regular serial arrangement of the large chambers extending from end to end. The post-larval condition is thus like that of the earlier larva in this feature; but the

* *Ann. des. Sci. Nat.*, t. xvi. p. 184, pl. iii. fig. 42. † HUXLEY, *op. cit.*

notochord has increased in diameter, and in transverse section is disproportionately large as compared with the slender character of the trunk in this species. The partitions stain deeply, but present no noteworthy histological features. A Clupeoid, double the length of the example just referred to, shows little alteration in the structure of the notochord.

During development BALFOUR states (No. 11, p. 456), "that most of the protoplasm with the nuclei is caused to pass to the periphery, where it forms a special nucleated layer, sometimes divided into special epithelial-like cells" of which he gives a figure in the case of the salmon, "while in the meshes of the reticulum a few nuclei surrounded by a little protoplasm still remain." RYDER mentions that he has not been able to see nuclei in the cells of the notochord;* but such appear to be present in *Anarrhichas*, since small granular areas, distinctly stained, occur frequently throughout. They are less definite than the nuclei of the newly-hatched salmon, which form large rounded or ovate bodies with granular contents, and nucleoli in the majority of the cells (Pl. XXVI. fig. 5). Moreover, the cellular rim within the sheath, as GEGENBAUR shows in the salmon,† is well seen in longitudinal vertical section in the wolf-fish, since it separates from the sheath as a deeply stained layer of cells of some thickness. In the post-larval *Cottus scorpius* ($\frac{3}{8}$ inch long) a single layer of large nucleated cells lines the chordal sheath, now firm from the deposition of hyaline matter. The central meshwork of chordal cells appears to be diminishing in diameter, and along with the cell-layer just named is separated from the hard sheath. A similar grouping of nucleated cells is very marked within the chordal sheath of *T. gurnardus*, $\frac{1}{4}$ inch in length; indeed, there are several features of interest at this stage of post-larval life, for external to the round nucleated cells‡ just mentioned, with their definite nucleus and clear cell-contents, is a layer of very much flattened cells. The large cellular spaces of the notochord have thin walls irregularly folded, and the more centrally situated chambers are more spacious than those outside. This condition is also well marked in the post-larval wrasse, about $\frac{1}{2}$ an inch in length, the larger cells being central. When $\frac{11}{24}$ of an inch in length the notochord of the post-larval Gadoid shows indications of vertebral divisions, dense transverse aggregations of nucleated tissue, flattened cells, and amorphous notochordal plasma, forming serial rings on the inner surface of the chordal sheath. As these ridges grow they rupture the hyaline sheath.

In the beginning of March the chief change in the notochord of the wolf-fish is the increase in the size of some of the median cells, those next the circumference being smaller. The nuclei, with their nucleoli, are also very distinct in many. Little alteration occurs in the general arrangement of the notochordal cells in May (Pl. XXVI. fig. 4), and though the development of the vertebral elements has made considerable progress, yet the cells show little or no modification of importance on the 20th of June.

*He writes—"In just hatched embryos of several genera I have as yet failed to discover any trace of nuclei in those portions of their walls which extend into the body of the chorda" (*Rep. U. S. Fish. Commiss.*, 1882, p. 511).

† *Elements of Comp. Anat.*, translated by Prof. JEFFREY BELL, p. 427, fig. 221.

‡ In prepared sections these cells recall precisely the appearance of the early blood-corpuscles in Teleosteans.

There is thus much less complexity in the stages just described than shown by BALFOUR and PARKER in the notochord of the Ganoids.*

Skull.—Much has been done in regard to the development of the cranium of Teleosteans, and the comparatively recent memoir of Mr PARKER† specially treats of the skull of the salmon, so that it will be necessary to give only a brief account in these pages.

On escaping from the ovum in January, the cranium of the wolf-fish is in a very rudimentary condition. The greater part of the vault is covered by a thin layer—the external cellular integument with a membranous layer beneath, the former showing a considerable thickening above the prominent ocular region similar to the tissue—consisting of pulpy columnar cells—in Gadoid larvæ $\frac{5}{18}$ inch long. In vertical section the first skeletal elements in this region are the anterior ends of the trabeculæ (Pl. XXIII. fig. 1, and Pl. XXIV. figs. 5 and 6, *tr*), which seem to have united in front, as in the salmon of the first day, and form a kind of ridge, with a superior convexity. They extend downward and inward, leaving a space behind the pituitary body, and appear to merge in the parachordals which lie on each side of the notochord. The notochord at its commencement abuts, in fact, on the cartilaginous plates just mentioned. The inner ends slightly curve upward, and do not appear to touch. The parachordals in the post-larval Pleuronectid, $\frac{9}{24}$ of an inch long, furnish a great contrast to this condition, for their inner edges have coalesced, and form a dense plate of cartilage—into a cylindrical cavity in which the anterior end of the notochord passes. From this dense central plate thus pierced by the oral end of the chorda, two thin plates pass and unite with the otocystic cartilage on each side. The basilar plate now forms a complete floor in the posterior cranial region. Even more marked is the united condition of the parachordals in the young Clupeoid, $\frac{3}{4}$ inch long, at the point where the notochord passes into the cranium—the coalesced part having, in transverse section, the form of a massive oblong element penetrated centrally by the notochord. Posteriorly, as the diameter of the notochord increases, the cartilaginous investing mass diminishes, until between the ears it is represented merely by four angular nodules of cartilage, two at the upper and two at the under side of the chorda. In the post-larval goby, $\frac{5}{24}$ inch long, the parachordals unite, but they form a comparatively thin, flattened, basilar plate, into which the chorda passes, and their lateral extensions unite with the otocysts and continue upwards over the hind brain—the posterior part of the chondro-cranium being, in fact, now wholly cartilaginous, and this complete tube of thin cartilage continues into the occipital region, and encloses the medulla oblongata. The small Gadoids, $\frac{5}{18}$ inch long, show a similar condition of the posterior floor of the skull, the thin cartilaginous parachordals uniting with the floor of the otocyst on each side; but the roof is still membranous above the fourth ventricle. There is a remarkable development of black pigment in the lining membrane of the otocystic cartilages—the corpuscles being situated

* The development of the vetebral elements of Teleosteans at St Andrews has been undertaken by Prof. D. J. CUNNINGHAM, of Dublin.

† *Phil. Trans.*, vol. clxiii., 1873, pp. 112–145, plates i.–v.

below the epithelial layer and the sensory cushions, and internal to the auditory ganglion, beneath which, and over the upper surface of the parachordal cartilages, it extends as a well-marked stratum. In the cod, $\frac{5}{18}$ inch long, the medulla is arched over by a deeply angular supraoccipital cartilage, having the form of an inverted V, and upon its sloping surface on each side a flat sheet of muscle passes. A little behind, these plates in the wolf-fish join a cartilaginous lamina, which bends upward and outward to form the floor of the auditory chamber on each side. In the median line above the tip of the notochord, and extending in front of it, is the infundibulum, but it disappears in the line of the laminæ forming the otocystic floors. After its disappearance the cartilaginous plates (parachordals) greatly increase in bulk, so that the notochord between them is strongly buttressed. Posteriorly, however, the density of the plates diminishes, and they spread outward, extending under the auditory sacs. Two thickenings occur here, one externally and another internally. With the former is fused the hyomandibular element. The thin band connecting the two parts mentioned gives way as one of the semicircular canals (probably the horizontal) comes in the line of section, and only connective tissue there unites them. They seem to be closely connected behind, though this could not be accurately made out. A similar disconnection is noticeable in the post-larval Gadoid, $\frac{11}{24}$ inch in length,—the basilar plate sending up ex-occipital elements to the upper posterior face of the otocysts, the cartilage of both being continuous, while below is a well-marked interval.

The tendency of the auditory capsule in *Anarrhichas* to sink downward is occasioned by the disappearance of the cartilaginous floor just described. The cartilaginous support of the notochord in transverse section now assumes the form of a broadly lanceolate process seated upon each side, the outer end abutting on the wall of the descending auditory sac, while the inner envelops the notochord. The cartilage curves upward fully half-way round the medulla, leaving the lower part of the notochord free. It then disappears, and the notochord, which has not at this point attained its full dimensions, is surrounded by perichordal connective tissue (by which also the side of the neurochord is clothed) supported by the muscle-plates.

An evident difference between the foregoing arrangement, and that in the salmon one day old, is the fact that the trabeculæ, while united and large anteriorly, diminish on their way backward, thin off in the middle, and then separate in the ocular region, becoming still less as well as more widely separated as they proceed backward. In the infundibular region, they again increase in size, but are separated by a considerable interval, and, shortly after the commencement of the auditory capsules, the anterior end of which is cartilaginous, a plate passes from them, with a slight obliquity upward and outward, and joins the cartilaginous boundary confined in this region to the floor and outer wall. The curvature of this floor quite differs from that in *Anarrhichas*, for, like *Gobius* and other forms, it is nearly flat. The hyomandibular, forming a buttress at this point, is narrow superiorly and more dilated inferiorly (more truly clavate) than in the wolf-fish. The pointed anterior end of the notochord now intervenes between the plates, which, however, do not touch it. Each plate somewhat behind this region becomes stouter; but the

lateral extension joining the ventral auditory plate diminishes, while the auditory capsule passes upward, and forms a dense structure superiorly—below the anterior semicircular canal. Then the basilar plates separate from the auditory capsules, and form, in section, an elliptical rod at each side, increasing in bulk further back, and again sending out a lateral plate to join the floor of the auditory capsule, and finally separating from it. Thereafter, each lengthens upward and outward, and joins the continuous cartilaginous mass bounding the auditory capsule posteriorly. Behind the latter capsule the cartilage passes upward from the sides of the neurochord, diminishing as it goes, nearly to the middle line of the dorsum. In sections further back we see it diminish to a lateral plate, pointed above, broad where it clasps the notochord, then broad above and pointed below, and still further back it disappears. There are material differences, therefore, in the cartilaginous elements of the two forms, one of the most marked being the larger size of the ear-capsules, and the deficiency of cartilage posteriorly in *Anarrhichas*, and the greater bulk of the cartilage at each side of the notochord behind the auditory region in the same form. The cartilage is evidently much more firm than in the salmon, and instead of collapsing the notochord, as before mentioned, remains circular. The cartilages of the posterior part of the cranium are, however, of greater complexity in the salmon. Further, in the latter form a slender bar represents the palato-pterygoid; but in the wolf-fish no trace of it is present. Its position in the salmon is very different, for, as Mr PARKER points out, it (his palatine) lies under the eye on each side, and each widely diverges from the other, whereas in *Anarrhichas* these bars are much nearer the trabeculæ.

Early in February (about the 10th) the pterygo-quadrate bar appears in *Anarrhichas*. In transverse section it has the form of a small cartilaginous rod in the anterior region of the snout (Pl. XXIII. fig. 1), just beneath the outer edge of the trabeculæ, which form a ridge in section. The bar seems to increase from before backward, and on 16th March the trabecular floor has gained so much in breadth, in the mid-region, that it lies on each side within the margin of the said floor inferiorly. Behind this, however, the trabeculæ form a narrow ridge, and the pterygo-quadrate bar passes outward on each side, and assumes an ovoid form in the subcutaneous tissue on the roof of the mouth. It is visible at this stage as far back as the pituitary body.

As development proceeds the anterior end of the trabeculæ becomes enlarged, and extends upwards in the olfactory region. This is distinctly seen on 16th March (Pl. XXIII. fig. 3).

On 6th April, a considerable vertical extension of the trabeculæ—most conspicuous a little behind the tip of the snout—has taken place. In transverse section it presents a somewhat hastate outline—broad and bluntly pointed below (with a median notch) constricted above this, and then slightly dilating upward. The united trabeculæ do not yet come in contact with the rounded anterior ends of the pterygo-quadrate bar, but after reduction in depth and assuming the shape of a broad inverted V, they reach the brain, and become continuous with a broad bar of cartilage passing upward to the dorsum on each side on the inner border of the eye. Beneath the anterior brain-mass are the crucial muscles,

and immediately behind the trabeculæ assume more of their earlier appearance, but with a median septum projecting superiorly. In *T. gurnardus*, $\frac{9}{24}$ inch in length, they send out a lateral expansion—a pre-orbital horizontal plate, but further forward they continue in the usual cylindrical form. Between the rod-like portion, which forms the main part of each trabecular element, and the lateral plate, a region devoid of cartilage-cells passes, the significance of which is not easily understood. As the ridge-like shape of the septum is by and by more marked in *Anarrhichas*, and as the cartilage diminishes, the median septum becomes a fibroid streak. The chief difference in the shape of the ridge-like bar of the trabeculæ is the slightly more bulbous condition of the outer edge in transverse section.

Before the infundibulum is reached, the trabeculæ become flat, and then separate, the bars in this case sloping from below upward and outward, and between them lies a firm plate of hyaline hard tissue, thickest in the middle and bevelled off as it approaches the trabeculæ. In front of the infundibulum a number of muscular bands pass toward the eyes in the middle line, and two blood-vessels soon after rest on the floor. At the infundibulum the hyaline floor diminishes, and the blood-vessels become more lateral in position. Behind the infundibulum the trabeculæ widen out and join the basilar plate forming the floor of the cranium, where the notochord commences. Thus they do not again unite. A further complication occurs about the beginning of May, when two slightly converging vertical bars of hyaline ossific tissue appear at the anterior ends of the trabeculæ—passing upward from the bases of the teeth, one dental sac being, indeed, placed between the limbs of the processes. The cartilage at this time is divided into an upper and a lower region, the latter again being vertically subdivided. The whole nasal region is cartilaginous, and further ossifications at the bases of the teeth are present. A plate of the same hyaline tissue appears in the free flap at the side of the mouth, and seems to represent the maxillary.

About the end of March a nasal cartilage develops behind the olfactory sacs, being, in fact, a superior process (fronto-nasal) of the trabeculæ at their anterior ends. A second bar of cartilage, the anterior end of the pterygo-quadrate, projects outward in horizontal sections, towards the outer angle of the truncated muzzle on each side—at a somewhat lower level.

The fronto-nasal plate in the post-larval Gadoid, $\frac{11}{24}$ inch in length, is very broad and massive, as indeed it is when the fish measures $\frac{5}{18}$ inch in length, but there now lie on each side externally two slender pre-frontal bars. The frontal rudiment appears in the young Clupeoid as a plate of cartilage passing transversely over the pineal region, and the fronto-nasal process below is flattened and less massive than in the Gadoids. In the herring, the frontal rods, passing superiorly between the eyes, broaden out before terminating over the cerebral lobes. Parietal rudiments appear in the gurnard, $\frac{5}{12}$ inch long, and a sharply pointed hyaline spine, firmly fixed to a horizontal base of the same dense tissue, occurs over these paired elements. When $\frac{9}{12}$ inch long the pre-frontal cartilages appear over the eye, outside the sclerotic cup, while below each eye are the infraorbital elements. The latter are well developed in the Gadoid $\frac{5}{18}$ inch in length. In *Callionymus*, $\frac{1}{3}$ inch long, the suborbital series arise as hyaline scales. In the

Gadoid of the size just specified, two hyaline plates pass obliquely on each side of the snout—separated by a small interval from the maxillary rods and external to the fronto-nasal cartilage. The maxillary elements, which at first are rod-like, become flattened at this stage, and may appear, *e.g.* in *Pleuronectes flesus*, $\frac{5}{12}$ inch long, as two lateral hyaline scales. The parethmoids are more median, and lie as two cartilaginous cylinders on each side of the stout ethmoidal (rostral) cartilaginous prominence. Above, the two optic cups are well advanced, and are also cartilaginous. Beneath the central parasphenoidal bar in *T. gurnardus*, $\frac{9}{24}$ inch long, a hyaline plate is formed, possibly the vomerine plate. In *Labrus*, $\frac{7}{16}$ inch long, however, is a similar median plate of hyaline tissue, but it is superior to the parasphenoid, and lies immediately under the point where the optic nerves cross. In the goby, as POUCHET long ago noted, "the maxillary elements appear in cartilage, and, when $\frac{5}{24}$ inch in length, develop a superior crest by a "kind of vegetation" of the cells (No. 119, p. 298), while further back an outgrowth in the form of a horizontal bar probably represents the pterygoid. In transverse section, therefore, two bars are present, an upper or pterygoid and a lower or maxillary bar. They have the same character, but are somewhat lengthened in a form $\frac{7}{24}$ inch in length.

The mandible of the young wolf-fish, on emerging in January, presents a less advanced condition than in the salmon. It forms a short conical process with a high cutaneous flap on each side. Though its cartilaginous and muscular elements are partly developed, it remains quite motionless, a feature doubtless connected with the widely-open mouth. MECKEL'S cartilage forms on each side a long curved bar, which slightly dilates at the anterior end, and terminates in a rounded portion—approaching that of its fellow in the middle line. The mandibular cartilage in *Callionymus*, $\frac{1}{3}$ inch long, is clothed on the ventral surface with dense hyaline matter, which thins out on the sides of the mandible. Outside the cartilage a separate hyaline scale exists, apparently developed in a deeply stained mandibular fold of the integument. In the gurnard, $\frac{5}{12}$ inch long, and in the cod, $\frac{5}{18}$ inch long, a similar extra-mandibular bar appears. It is very massive in the Gadoid, $\frac{1}{24}$ inch in length, as well as very prominent in section, since it and the surrounding tissue of the flap stain deeply. An element is seen above MECKEL'S cartilage in *Callionymus*, $\frac{1}{3}$ inch in length, probably the symplectic. Posteriorly in *Anarrhichas*, the mandible gradually dilates, and at the articular region forms a slight hollow for the rounded end of the quadrate, the cartilage being continued further back as an angular plate, somewhat broadly lanceolate in outline. The quadrate seems to be a narrow bar supported behind by the pointed end of the symplectic—continuous with the hyomandibular cartilage. Along with other changes, the mandible becomes much lengthened in March.

At the seventh day in *Anarrhichas*, little elevations appear in the jaw, and towards the end of the month one or two simple conical teeth, similar to those in the salmon, present themselves in a line anteriorly. These increase in number, still keeping in linear order in April, though the yolk is of considerable size. In the free condition the salmon feeds readily in this state, the most abundant form found in the stomach being *Cyclops*. Thus both fresh-water and marine larval fishes feed upon similar food. The teeth

increase both in number and size at the sixth week, large recurved teeth appearing on the hyoid, while the pharyngeal cartilages are similarly studded.

Both wolf-fish and salmon, on hatching, are, however, devoid of teeth; but developmental changes seem to be more rapid in the latter than in the former, the cartilages apparently being more actively plastic, and the advanced stage at which exclusion from the egg takes place afford greater time for maturity. Thus at the seventh day MECKEL'S cartilages are separated by a cellular band in front, while they are less rounded than in *Anarrhichas*. A short distance behind is a line marking off the articular piece. Four teeth are visible, symmetrically placed and developed from the mucous membrane in the usual manner. The first presents a glassy coat of ossific matter, forming the point and sides; beneath this a narrow layer of dentine occurs, while the centre contains the cellulo-granular pulp continuous with the oral mucous membrane. It is placed behind the symphysis, and is slightly inclined backward; the second is larger and stronger, with a more decided backward curve, while the third is a straight tooth about the size of the first; the fourth is similar, but shorter. In the upper jaw are ten teeth; but all that can be said is that four lay in proximity to the maxillæ, two (vomerine?) intermediate, and two at a greater distance.

Pleuronectes flesus, when $\frac{5}{12}$ inch in length, has numerous teeth in both the upper and lower jaws. They pierce the oral mucous membrane as acutely pointed hyaline structures; the mandibular cartilage at this time being completely encased in hyaline tissue, and sending down from its inner ventral margin a sharp crest of the same hard substance, while the teeth occupy a corresponding position on the inner margin superiorly, and have their points directed inward. Numerous papillæ with developing teeth also occur. The pharyngeal teeth in the post-larval goby, $\frac{7}{24}$ inch in length, and in *Labrus*, $\frac{7}{16}$ inch long, show interesting stages of growth. In the former species, on both the floor and roof of the pharynx, the dental sacs are crowded together; but in *Labrus* they extend along the under surface of the basi-branchial plate, as well as on the pharyngeal floor. Each tooth-sac is formed of deep columnar cells, in which the conical tooth is seated on an internal cellular pulp or papilla. The tooth is formed as a hard hyaline cap—semilunar in transverse section—which becomes more conical, and finally, when very acuminate, pierces both the sac and the epithelium of the pharynx. At the tip the tooth is solid, and a little below a neck or ring of clear deeply-stained tissue exists, the hollow portion or root of the tooth beginning at that point. Some of the teeth appear to be compound, and give off one or more denticles from a common papilla enclosed in hyaline tissue; while in other cases separate teeth occur, in such close proximity that three or more may be present in a single fold of the pharyngeal epithelium. The teeth may lie deep in the pharyngeal wall; indeed, some of these structures in a young post-larval *Labrus* are separated from the pericardial chamber underneath merely by the thin pericardial layer, and in this species the subepithelial tissue of the pharynx is in some parts little else than a mass of tooth-sacs. In the post-larval gurnard, $\frac{5}{12}$ inch in length, the cartilaginous mandible is completely surrounded by hyaline tissue, and in some of the microscopic

preparations it appears that this tissue is formed in the perichondrial cellular coat; indeed, near the symphysis the very small deeply stained cells clearly intervene between the hyaline deposit and the cartilage itself. The hyaline matter, moreover, does not in transverse section exhibit the same cylindrical form as the mandibular bar; for, though rounded on the outer side, it rises into a blade-like ridge on the inner side, while above its surface is flattened.

The maxilla in *Salmo* presents a different appearance from most of the other cartilages, since the cells are indistinct, the markings resembling irregular waves, except at the anterior and posterior ends. Between the sixth and seventh weeks the dentary region of the mandible shows many teeth, arranged in several rows, the anterior being curved, the posterior more or less straight. About thirty teeth occur on the premaxillæ and maxillæ. The mucous membrane is raised into papilliform elevations, the summit of each bearing a tooth. The premaxillary teeth are the largest and strongest. The otoliths are at this stage the only hard and dense structures in the cephalic region, and they are somewhat spherical, and present the usual radial striations. The posterior otolith in each auditory sac is irregular, and shows longitudinal markings and interrupted streaks. The cells of the cranial cartilages are, on the whole, more regular and distinct than those of other parts.

Hyoid Arch.—The embryos of the wolf-fish which issued on 17th January presented a well-developed hyoid arch. The glosso-hyal region has anteriorly a large cushion of mucous tissue. Three cartilaginous elements form a rounded arch within the latter (Pl. XXV. fig. 1), viz., a median (glosso-hyal) and two lateral (hypo-hyal). The cerato-hyals abut on the hypo-hyals. In all these the cartilage-cells are smaller than in the salmon. The cerato-hyals are considerably less than in the salmon, and, indeed, the same may be said of the cartilaginous elements in general, and especially of the glosso-hyal. Four branchial arches succeed the former, and bear simple though highly glandular papillæ (Pl. XXV. fig. 2). The fifth arch is visible in a specimen on 20th April, as a bar on each side in front of the pericardial chamber, and teeth are readily distinguishable on 1st May. The double rows of branchial pinnæ present deep crenations along the sides in April, and these form long papillæ towards the end of the latter month and in May, so that each process is feather-like. Hyaline ossific tissue now appears as a superficial coating upon the surface of the branchial cartilages. On 21st May the cerato-hyal and other cartilages of this region are bordered with a firm layer of the same tissue. The brittleness of the branchial arches externally shows that this development has made considerable progress, and the ossific investment is still more marked a month later (20th June), when it was difficult to make good sections, on account of the brittle character of the skeletal bars, or rather of the hyaline ossific tissue clothing them. The branchial papillæ at this latter date are richly pinnate.

The hyoid bar may, as in the gurnard, $\frac{5}{12}$ inch in length, rapidly lose the form of a simple rod, and while the mandible is rudely elliptical, the hyoid becomes bilobate in transverse section, from the presence of deep grooves, and shows two prominent outer

ridges and one superior internal ridge. The operculum in the various post-larval forms presents no noteworthy points, except in the wrasse, $\frac{7}{16}$ inch in length, in which a dense plate of hyaline tissue appears in the tegumentary flap.

Vertebral Column.—The first of the permanent skeletal structures in connection with the notochord in *Anarrhichas*, are a pair of cartilaginous bars, which spring from the upper side of the perichordal sheath at the sides of the spinal cord. These are developed in a streaked, cellular region (mesoblastic) very evident beneath the muscular masses of the parts. Each bar springs by a broad base from the notochordal sheath, passing upwards to form an investment round the spinal cord. Early in February, a more regular arrangement of cells takes place at the base, which is triangular in transverse section, and in the investment, passing upward laterally, a transverse disposition of cells occurs, forming indeed a cartilaginous bar—the neural arch. The firmness of this buttress on each side dorsally, is probably the reason why the unprotected median arch of the notochord bends upward in the preparation; and the precursory thickening at the sides inferiorly produces the same result in the ventral arch. At this time there are no distinct interspinous cartilages, though there are signs of them dorsally. These structures, however, appear in March, and towards the end of that month the neural arches meet superiorly over a small canal, which has for some time been visible in the region. Posteriorly they also send up dorsal processes—the neural spines. Above the latter is the interspinous cartilage; but the two do not touch.* In the beginning of April, a somewhat conical cartilaginous process appears at a corresponding region in the lower arch, but proceeds only a short distance downward above the segmental duct, being larger, indeed, in the posterior than in the anterior region of the body. It gradually lengthens so as to pass downward and outward over the subnotochordal region in which the artery and segmental ducts lie. By the end of April, or early in May, these processes are strengthened by a coating of hyaline ossific matter, continuous with that which has invaded the notochordal sheath (Pl. XXVI. fig. 3, *ncs*). Instead of collapsing or becoming wrinkled in sections, the sheath forms a firm, nearly circular ring. This hyaline and structureless ossific matter, like that seen in the premaxillary and clavicular elements, surrounds the conical process of cartilage, so that in several sections it forms an isosceles triangle, with a long apical process. The two dorsal arches are similarly coated with this matter.

In post-larval stages of other Teleosteans, considerable variation in the character of the elements of the early vertebral arch exists. In *Cyclopterus*, for instance, the basal stumps of the neural arch arise as cartilaginous processes, developed as in *Anarrhichas* within the perichordal sheath, and resting upon the chordal investment. In the young cod, $\frac{5}{8}$ of an inch in length, the neural arch, as in the wolf-fish, appears to spring as a hyaline outgrowth from the tubular investment of the notochord, which is formed of the same hard tissue. In *Cottus scorpius*, when only $\frac{3}{8}$ inch long, the notochord exhibits this

* These probably correspond with Balfour and Parker's "two bars intervertebrally placed,—two osseous plates on the outer side of these, and continuous with the lateral osseous bars of the neural arch. The former give rise to cartilaginous elements above the osseous bridge of the neural arch in the adult."

hyaline coat, having the form of a translucent ring, in transverse section, separated by an interval from the inner limiting cells of the chorda itself. The neural arch is imperfect at this stage; but the hæmal arch, formed of the same hyaline matter, is complete in the anal and caudal regions. It is remarkable, that in the tail, the elements of the neural arch are formed of cartilage, upon which hyaline matter appears as a thin shell; but anteriorly the arch is formed by hyaline outgrowths solely. A similar condition is exhibited by *Cottus quadricornis*, when $\frac{9}{32}$ inch in length, the cartilaginous outgrowths destined to unite as the neural arch in the caudal trunk, having at first a plate of hyaline matter deposited on the outer surface only. In the post-larval *Labrus*, $\frac{7}{16}$ inch long, while the anterior part of the spinal cord is protected incompletely by the developing neural arch, consisting of hyaline basal stumps, and an independently formed hyaline neural spine, bifurcate below, the posterior portion of the cord in the tail is still enclosed merely in the membranous chordal sheath, destitute of any more permanent element than the rudimentary neural spine, which consists of two approximated plates of hyaline matter, clothing a strand of connective-tissue. This strand forms dorsally a knob, which is deeply stained in the microscopic preparation, and continues to the base of the dorsal fin (in this species characteristically lengthened), where a second pair of hyaline plates are developed, viz., the rudiments of the terminal fin-rays. The hæmal arch below is complete, and encloses what appears to be a mass of cartilage, so that it is really a solid ventral process, below which pass the caudal artery and vein. In the caudal fin the same features are seen, but the connective-tissue strand which passes down from the hæmal arch is clothed by hyaline matter, two lengthy plates of which form a large hypural, and upon their outer surfaces a diagonally directed muscular band is inserted on each side. Each muscle is attached to the corium about the level of the hæmal arch, and passes obliquely downward.

The cellular external region of the notochord in *Anarrhichas* is rendered conspicuous by the appearance of the definite hyaline ring above mentioned. A similar ossification proceeds in the dorsal fin-rays, in fact, they appear to commence as hyaline bars; but the interspinous elements seem not to do so. The neural spine is likewise ossified. All the structures mentioned have become more ossified at the beginning of May, the hæmal arches meeting posteriorly to enclose the artery and support the interspinous elements of the median ventral fin with its fin-rays. The hæmal arches in the region near the caudal become elongated, the posterior pair being also greatly flattened, for the support of the caudal rays.* At a still later stage, towards the end of May, the hæmal spines have frequently between them a transverse row of cartilage-cells, apparently binding them together towards the tip, the evidence of a series of sections showing that amalgamation has taken place. The ossified sheath of the notochord is now brittle, and frequently gives way under the knife of the microtome. At this stage no special lamellæ leave the various ossified structures connected with the vertebral column, as GRASSI† shows in

* The firm hyaline ossification here mentioned is by the process called ectostosis. When surrounding the chorda in the wolf-fish, it recalls the unsegmented cartilaginous tube BALFOUR found round the notochord of Elasmobranchs.

† "Lo suiluppo della colonna vertebrale né pesci ossei" (*Mem. del dott.* BATTISTE GRASSI; *Atti d. R. Accad. dei Lincei*, ser. 3, vol. xv. pp. 311–337, Taf. i.–viii.).

the salmon, and it is clear that in all in these parts the ossification is external to the cartilage, to which it forms a coating. The dorsal and neural arches present numerous cartilage-cells inside the osseous investment, where they spring from the column, but a transverse row of large cartilage-cells occurs beyond this, and the whole at the end of May is enclosed by a dense hyaline ossific layer. This hyaline sheath can often be cut without fracture, so that it contains certain plastic elements.

At the latest stage examined (as shown in specimens that survived till nearly the end of June), after maceration, the vertebral column is found to consist of rings of firm hyaline osseous tissue of considerable thickness, with spaces between the serial vertebræ. To the dorsal and ventral aspects are attached the neural and hæmal arches, which meet and give rise to the spine. At the junction of these arches is a groove marked with transverse striæ—an aspect probably due to the remains, still visible, of the cartilaginous elements. A similar translucent region occurs at the base of each pillar of the arch, at the vertebral ring, and probably arises from the centre, now wholly removed. A comparison of this with the vertebral column of the young cod, obtained in tidal creeks in the beginning of June, will show how advanced the latter species is. The vertebræ of the cod are ossified from end to end externally, even more so than is indicated in Grassi's figure of the bleak (*op. cit.*, pl. vii. fig. 8), so as to be separated only by a thin intervertebral edge, and the notochord is reduced internally to a moniliform band.

In the newly-hatched salmon, cartilaginous spines, neura- and hæmapophyses, occur on each side of the notochord above and beneath. They are fixed to the sheath of the notochord, penetrate one-third its depth, and are best marked anteriorly. About the sixth week the vertebral column presents a moniliform appearance, the neura- and hæmapophyses being adherent, but not continuous. Under pressure a tough moniliform cellular central portion escapes,—the remnant of the notochord. The column has now a distinctly barred appearance from the development of the vertebræ, each vertebral bar, moreover, bisects the nail-shaped head of the neura- and hæmapophyses. These last named elements are exactly opposite each other in the darker portions, and on reaching the column the terminal process expands into a nail-like head, having on each side a pointed tip, devoid of cartilage-cells. The processes retain nearly the same shape as formerly described at a much earlier period. At the present stage, however, the cells are smaller and more crowded, and their nuclei are more distinct. At the tips of the larger ones, near the tail, the cells are smaller, and more flattened, as well as more densely arranged. Grassi* enumerates in the salmon and others four layers from within outward,—(1) cellular stratum of the notochord, (2) epithelial coat, (3) proper membrane of cord, (4) fine elastic amorphous membrane,—which is developed from the surrounding embryonic connective-tissue.

Ribs.—Little can be said in the way of addition to information already existing as to the development of the ribs. They form long bars of finely cellular cartilage, at the stage of date—20th June, when the ring of hyaline ossific matter surrounds the notochord,

* *Op. cit.*

and, as Balfour and Parker observe, they are modifications of hæmal processes, as indeed had previously been noted, amongst others, by Müller and Gegenbaur.

In the salmon, at the sixth or seventh week, cartilaginous ribs are present, and show a well-formed head articulated to the parapophyses by a broad surface, apparently having some elevations on its otherwise straight edge. The attached end is widened and shows numerous cells; but distally a single row of cells gives the tip a scalariform appearance. In a few instances, the cellular structure was disconnected in the centre of the rib, the intervening band consisting solely of a cord of the transparent matrix. The same has been noticed by Grassi in a Cyprinoid.

Brain.—In *Anarrhichas*, as in most Teleosteans, the chief features in the brain are the great size of the mesencephalon, and the depth of the entire brain-mass. Probably connected with this is the much more marked flexure of the anterior end of the notochord (Pl. XXIV. fig. 1) in the larval wolf-fish than in the salmon. The fore-brain is shorter in its antero-posterior diameter, and presents a comparatively larger area (in transverse section) than in the salmon. At the origin of the optic nerves the proportional area of the brain-surface is larger, and the breadth of the roof (mid-brain) greater than in the salmon.

The shape of the brain-mass shows, indeed, great variation in post-larval stages of various species. In the cod, $\frac{5}{18}$ inch long, it is, like *Anarrhichas*, rounded and compact as a whole—the optic lobes in cross-section forming a semicircular mass—almost equally composed of an upper layer of white matter, and a lower layer of deeply-stained vesicular matter, the line of separation between them passing parallel to the surface of the lobes. Posteriorly the roof and floor of each optic lobe thins out very much. In the post-larval stage of the gurnard, about $\frac{5}{12}$ inch in length, the form of the brain is very different—the conformation of the cranium being much flatter than in the Gadoid—the brain-mass, especially the optic lobes, are markedly depressed and of disproportionate superficial extent, and much thickened in the lateral portion. The vesicular and white unstained parts form two well-marked strata of about equal thickness, a condition just noted in the optic lobes of the Gadoids. As might be anticipated from the form of the adult head, the post-larval *Callionymus*, $\frac{1}{3}$ inch long, shows a brain considerably depressed, especially in the middle line; but in the herring, when of slightly less size (viz., $\frac{7}{24}$ inch), the flattened condition is even more remarkable, the optic lobes spreading out laterally, and having thus a large superficial area. Hardly less striking is the condition of the optic lobes in a form, probably *Ammodytes* ($\frac{1}{4}$ inch long). They are more rounded, but, on account of their disproportionately large size, present a superficial surface quite as noteworthy as the preceding forms. The deeply-stained vesicular matter forms a much thicker stratum than the unstained white layer, and the line of separation is somewhat irregular, and does not pass parallel to the superficies of this region of the brain. These two layers in the optic lobes of the goby, $\frac{5}{24}$ inch long, differ still more from the Gadoid and other examples mentioned above, the vesicular stratum in transverse section passing upward to a median point, and forming a deeply angular mass of great thickness, sharply marked off by the sloping line of separation on each side from the thin and

dorsally-rounded whit estratum above. The apex of the grey substance in this early post-larval stage quite separates the white matter into two masses, and this condition is still more marked in a later post-larval stage, the vesicular matter intruding to a larger extent in the goby $\frac{11}{24}$ of an inch in length.

The superior fold of the mid-brain (optic lobes) in *Anarrhichas* forms from side to side a semicircle, and is therefore larger than in the salmon. Moreover, the prolongations of this fold on each side towards the cerebellum are longer than in the salmon. The adjoining edges of the optic lobes (forming the sulcus longitudinalis superior) are somewhat regularly and deeply crenated, as if indicating rudimentary convolutions. The posterior mesial fold (valvula) of the same region is likewise larger, and it gradually widens out posteriorly until it merges in the furrow of the medulla.

Anteriorly the brain presents two somewhat short cerebral lobes, with a large median ventricle, which terminates a little behind the anterior border. In vertical transverse section they are seen in Pl. XXIV. fig. 5.

The lower margin of the cavity of the fore-brain is closed by a thin cellular layer in the middle line in front of the optic commissure. A well-marked commissure passes between the two lobes a little above the inferior border posteriorly, and the fissure in transverse section is thus closed up inferiorly in the region (Pl. XXIV. fig. 5, *ac*). In the section, however, only a portion of the commissure is visible. This may be, as Balfour and Parker suggest in *Lepidosteus*, the homologue of the anterior commissure. The olfactory nerves (Pl. XXIV. fig. 4, 1) spring from the anterior end of the cerebral lobes, and their separation is well shown in the same figure.

Very soon afterwards the optic fibres from the lower part of the brain cross (without decussation) in the middle line.

At the end of March the optic nerves are hollow in some, a considerable chamber occurring in the centre from the choroidal fissure to the optic commissure. It must be stated, however, that in earlier stages this was not always visible, probably because the degree of development varied so much.

While in many post-larval forms, *e.g.*, the goby, when $\frac{11}{24}$ inch in length, the optic nerves are solid; in the gurnard, $\frac{5}{12}$ inch in length, they exhibit a well-marked longitudinal fissure shortly before penetrating the sclerotic layer to enter the optic chamber. This chamber is even more distinct and capacious in *Labrus*, $\frac{7}{16}$ inch in length, and at the point where the nerves pass over each other the lumen is of an irregular form, as its walls are much wrinkled, the hollow nerve showing a series of folds, which disappear as it passes outward, the walls approaching so as to enclose merely a narrow median slit, and this can be traced only to the aperture through which the nerve enters the eye. In *Callionymus*, $\frac{1}{3}$ inch in length, the optic nerves are surrounded by a layer of fibrous tissue having a slightly metallic lustre.

Some further points of difference present themselves in regard to the olfactory nerves in certain stages. Thus, after they have separated from thefore-brain in the manner described in *Anarrhichas*, they may pass downward to penetrate the lateral wings of

the trabeculæ, as in the post-larval gurnard, $\frac{5}{12}$ inch in length, in which species the fronto-nasal cartilage is very dense and massive. Through this cartilage the nerve goes by a distinct canal—a similar canal, it may be noted, passing along a parallel course slightly external to the nerve, and giving transit to an artery. In the cod the nerves pass along the floor of the cranium, and, without piercing the anterior trabecular outgrowth, reach the olfactory pits. The nasal pits show considerable variation in their rate of development, *e.g.*, in a Clupeoid barely $\frac{1}{4}$ inch long, in which a cartilaginous cup is already fairly formed beneath the olfactory organ; but in the goby, about $\frac{1}{2}$ inch long ($\frac{11}{24}$ inch), the walls of the chamber, though very thick and composed of elongated radially-arranged sensory cells, have merely a very thin outer membranous support similar to the delicate layer lining the pit. In the outer portion of the wall of the organ large loosely connected cells appear, forming a distinct prominence, probably indicating the transverse bridge, the later development of which in *Anarrhichas* is described on p. 918. The cartilaginous optic cup is well developed in the early post-larval stage of *Pleuronectes flesus*, that is when the young fish measures $\frac{5}{12}$ inch in length.

Behind the optic commissure in the wolf-fish a strong band of fibres passes from side to side along the ventral edge of the brain (Pl. XXIV. fig. 6, *fa*), forming a broad bridge of communication. It disappears about the commencement of the succeeding region. The roof of the anterior cerebrum is composed at first of a layer of nerve-cells, which becomes thinner as the chamber above the inferior pale median streak becomes larger. So thin is it in a line with the anterior commissure (Pl. XXIV. fig. 5) that, if it is no better developed in the Ganoids, WILDER would very readily suppose it to be absent. There can be no doubt, however, of its presence in the Teleostean embryo, for the spindle-shaped cells can be followed upward to each edge, as a diminishing column that runs into the thin layer of more flattened cells forming the roof. It is certainly remarkably thin in some parts. It rapidly increases in thickness as the thalamencephalon is approached (Pl. XXIV. fig. 6, and also in Pl. XXIII. figs. 3 and 3*a*). As in the Ganoids, a transverse commissure appears in front of the pineal gland on the roof of the vesicle formed by the anterior portion of the thalamencephalon. Posterior to the gland are other bands of fibres (Pl. XXIII. fig. 3) crossing over the arch beneath the optic ventricles, and above the continuation of the third ventricle. Behind the foregoing is the large posterior commissure, which in front commences over the infundibular region, and it increases in size when traced backward.

The optic lobes posteriorly form a conspicuous vesicular region on each side, from the great size of the optic ventricles, and on the floor, in its progress to the median fold, are the tori semicirculares (Pl. XXIV. fig. 3), fusiform thickenings very characteristic of the region over the commencement of the notochord. The arrangement of these folds in *Anarrhichas* is noteworthy, and differs from the same folds in the salmon whether one, thirteen, or forty-five days old, but the nature of the preparations may account partly for the divergence. The latter species (salmon) shows a nearly straight section of the floor of each optic lobe posteriorly, and the fusiform enlargements and distinctness of the median

dorsal folds (valvula cerebelli, fornix of GOTTSCHE, which seem to be present only towards the posterior border) are all much more evident in *Anarrhichas*. Behind this, the inner or inferior surface of the outer layer becomes richly folded, while the fusiform condition of the lower fold disappears, a nearly straight band taking its place. These folds continue until the optic ventricles disappear. In the salmon of the first day there are only a few smooth folds on the under surface of the roof of these lobes.

In the region of the pituitary body in *Anarrhichas*, the trabeculæ are more elongated and more obliquely situated than in the salmon, where they are also more widely separated. The pituitary body is perhaps less flattened from above downward than in the salmon, but in both forms it has the same structure, viz., aggregated nucleated cells (Pl. XXIV. figs. 1 and 2). A band, apparently of connective-tissue, proceeds from the under surface of the brain to the pituitary body, and this band is in the main fibrous; while in the salmon it is composed of connective-tissue cells, the nuclei of which stain very deeply. A layer of connective-tissue separates it from the infundibulum.

In each of these forms the pineal gland—both as to position and histological structure—is the same, but the pale commissural fibres passing to the upper region of the mid-brain are proportionally larger in *Anarrhichas*, and therefore can be traced further into its substance (Pl. XXIV. fig. 1, *pf*). The central aperture of the thalamencephalon in front of the pineal gland is more capacious and better defined than in the young salmon, and it rapidly assumes large dimensions, and opens into the third ventricle inferiorly (Pl. XXIII. fig. 5, and Pl. XXIV. fig. 2). The ventricles of the optic lobes appear superiorly at the side, as in *Anarrhichas*, and the two rapidly merge into one chamber. The separation of the infundibulum from the peduncular region is more distinct, the connective-tissue being very apparent; but the arrangement of the parts is similar to that in the wolf-fish, though the infundibular cells are larger.

The complexity of the brain, especially in regard to minute structure, augments as the larva increases with age. Thus, in the middle of March the radiate fibres of the mid-brain (optic thalami) to the optic lobes are largely developed, and the thicker cortical region is more clearly differentiated from the inner layers. Moreover, it is evident that the tori semicirculares posteriorly are now encroached upon by commissural fibres passing to the roof.

A distinct and broad commissure appears in front of the pineal body, and is continued behind it, the posterior band being very evident, so that it may even be regarded as separate. Horizontal sections do not, however, sufficiently aid in deciding this point. Next, from before backward, is the commissure of the optic nerves inferiorly and in the neighbourhood of the infundibulum. Lastly, are other transverse bands which will be subsequently mentioned.

Somewhat later a differentiation appears in the centre of the peduncular region, in the form of a rounded area with a cellular margin (Pl. XXIII. fig. 6); the vesicle in front and beneath the pineal gland becomes more or less obliterated; and the optic ventricles posteriorly show a diminished lumen on each side, for the fibres passing to the

outer border of the fusiform tori semicirculares, and in part through them, considerably encroach on the cavity and bind the roof more closely down. On 20th June a more distinct differentiation of the anterior ends of the fore-brain into anterior cerebral and olfactory lobes (Pl. XXIV. fig. 4) is noted, and the area behind is more complex, cells being developed chiefly on the upper and inner edges, that is, on the sides of the median ventricle as seen in transverse sections. The median arch or roof of the fore-brain is considerably narrowed in front by the great increase in the nerve-mass at each side, so that a mere chink remains. On each side of the central fissure superiorly the margin of cylindrical cells trends upwards, and ends in a point, then bending outwards, leaves an acuminate projection in transverse section. Externally the arch is completed by a layer of tissue containing pigment—continuous with the "pia mater," and internally by another layer, similar in structure, and therefore differing in appearance from nerve-tissue proper. This indifferent tissue is probably the anterior boundary of a chamber or vesicle which immediately appears in the median line in front of the pineal gland, and is possibly homologous with that described by Balfour and Parker* in the roof of the thalamencephalon in *Lepidosteus*. The vesicle is preceded by a double papilliform process of the roof, which apparently soon coalesces inferiorly to form the vesicle. The entire process is formed of nerve-cells, and when the vesicle is fully developed, these present in transverse section a somewhat columnar arrangement, and the wall is symmetrically folded superiorly. The band of nerve-tissue forms the floor of the vesicle or chamber just mentioned and the roof of the ventricle, for the anterior lobes present a peculiar layer of large nucleated cells under the columnar series lining the thalamencephalic chamber. This is especially noticeable in the line of the section shown (under a low power) in Pl. XXIII. fig. 3*a*. The walls of the vesicle are quite distinct from the optic thalami at the sides, but gradually (as we proceed backward) they merge laterally into the optic thalami, then the roof becomes a mere bridge between them, each end being thoroughly incorporated with their tissue; while the floor, assuming a doubly fusiform shape (*i.e.*, thinner in the middle and at each end), soon disappears. In the drawing (Pl. XXIII. fig. 3) the separated ends of this floor are seen—the knife having probably caused rupture. When it (the vesicle) first appears in section comparatively little brain tissue lies externally and very little inferiorly, while superiorly only the thin roof of the vesicle occurs under the pia mater. Proceeding backward the nerve-substance (optic thalami) at the sides becomes massive, and the vesicular space enlarges in the median line. Moreover, a papilliform process (pineal gland) makes its appearance in the centre over the roof of the chamber. A succeeding section (Pl. XXIII. fig. 5, possibly somewhat oblique) is instructive, showing the tapering points of the mid-brain touching in the middle line, the cellular pineal body appearing immediately beneath, while along the roof of the thalamencephalic chamber a commissure connects the central pale fibrous region of the commencing optic thalami on each side. An unusual development of connective tissue (neuroglia) could only be confounded with this connecting band, and

* *Phil. Trans.*, 1882, pt. ii. p. 376.

there seems no reason to alter the view just mentioned.* Moreover, this commissural band of fibres is observed in several succeeding sections as it spreads over the roof of the ventricle between the optic thalami, the sides of the chamber being now solid masses of nerve-tissue (optic thalami). This section further indicates the opening of the thalamencephalic vesicle or chamber into the common (or third) ventricle, extending to the anterior lobes in front and the optic thalami in the region under consideration. In the next section a cellular band proceeds in the median line of the roof towards the margin of the arch, apparently the remnant of the pineal gland formerly mentioned, a few of the commissural fibres being still visible beneath. Just behind, the median parts of the lobes of the mid-brain become broader, and are separated inferiorly from the central process; moreover, fibres pass between them and through the median process, forming a distinct commissure. A space lies on each side of the latter inferiorly, the roof being formed by the lobes, the floor by a more or less fibrous band on each side connected with the median process between the lobes (Pl. XXIII. fig. 5). An indication of a space, possibly due to the mode of preparation, occurs below the latter band, viz., at the point marked *sp.* on Pl. XXIII. fig. 5, and then the cells forming the lining of the great central ventricle in the thalami occur. As the commissural fibres last spoken of diminish, the central body becomes more clearly differentiated from the edges of the lobes of the mid-brain, so that it is somewhat awl-shaped, narrower above, where it joins the lobes in the middle line, dilating in the free middle region, and again narrowing at its attachment to the roof of the inferior region of the mid-brain. In structure this median region is cellular. In the next section it is bell-shaped, the handle of the bell being superior. The cells are also symmetrically arranged, viz., a thick layer of large cells externally along the margin of the bell, and a broad median band of large cells. The latter arrangement, which is broadest inferiorly, may indicate a double process (*i.e.*, the coalescence of a structure originally double). The sides of the structure become continuous inferiorly with the floor of the mid-brain (optic thalami), and its base rests on the commissure (with the probably artificial aperture), for separation of the two strands might easily occur in the lax tissue (neuroglia). This separation of the commissure into two layers is a marked feature, and cells occur between them as they debouch into the thalami (Pl. XXIII. fig. 5). Posteriorly the median process becomes more cylindrical, narrows inferiorly, then hangs like a leaf-shaped structure from its stalk between the optic lobes, its double nature being shown by its pale central region on each side and the two rows of median cells. It diminishes to a mere papilla and then disappears.

The commissural fibres between the optic thalami (in the larva of 20th June) appear in transverse section along with the pineal gland; they are thus in the same plane, and not in front of it, as in the Elasmobranchs, and at first they have a median cellular mass, which is torn in the preparation studied—causing the cavity before mentioned. The pineal gland lies above the fibres, and below them is the fissure of the mid-brain continuous with the Aqueductus Sylvii. The fibres are thickest towards the posterior part of the gland.

* What connection this commissural band may afterwards have with the pineal gland is uncertain.

The commissure on the roof of the lower division of the mid-brain (thalami) forms a uniform deep band after this, and then it ceases, so as to open up the whole central region into a single chamber (common ventricle).

In longitudinal sections the roof of the thalamencephalon shows a large fold of cells (tela choroidea) in front of the pineal gland. The latter is cellular (on 1st May), and is connected by strands of fibres at its base with the centre of the optic thalamus, the direction of the fibres being generally downward and backward.

At this stage the posterior region of the fore-brain is protected externally by a special plate of cartilage, which stretches over and extends for some distance down each side, passing over the anterior end of the optic lobes. The black pigment lies beneath it, while externally is a hyaline ossific stratum. In transverse sections a deep dimple is usually present over the pineal gland. The next feature of note is the formation of the optic commissure. This is produced by a great band of fibres arising at the upper border of the thalamus, and apparently continuous with the optic lobes above. This massive band passes down on each side of the central region of the thalamus and the fibres simply cross each other beneath. A streak in the centre of the band inferiorly is probably the lumen of the nerve-trunk, and it can be traced to the choroidal fissure. The succeeding sections show oblique bundles of longitudinal fibres on each side of the central region inferiorly. These are isolated by the vertical bands, some of which form a commissure beneath the central chamber of the thalamus. In the line of the great transverse commissure, just behind the pineal gland and at the upper part of the thalamus, a circular region appears in the centre of the lateral mass of the organ superiorly, which increases in size as it proceeds backward. Its outer (cellular) region stains deeply, and in the preparation it has separated from the surrounding tissue. Vertical bands of fibres pass across each region in front of the pituitary body. Shortly after the latter appears they diminish in size, and, keeping at the upper part of the infundibulum, disappear before the pituitary slices do. By the differentiation posteriorly of the upper region into crura cerebri, these rounded bodies are placed in transverse section at the upper part of the infundibulum. The lateral fissures from the infundibulum appear before the former cellular differentiations cease, and they by and by attain a larger size than the central one, apparently from constriction of the latter. This arrangement indicates a possible homology with the trifid infundibulum of the Elasmobranchs, and the so-called lobi inferiores are thus apparently closely connected with the infundibular apparatus. The central fissure of the infundibulum has a very definite contour, and, inferiorly, it leads to the pituitary body, above which a lozenge-shaped dilatation occurs, the margin of the aperture being directly continuous with the hypophysis, the centre of which is dimpled superiorly by the tip of the lozenge-shaped space. By and by (proceeding backward) this central infundibular aperture becomes trifid by the protrusion of lateral diverticula, each forming a separate pouch after the connection with the pituitary body is broken. These diverticula soon disappear and the central aperture becomes very small, and at the same time its walls are folded and defined by cylindrical

cells. The folds then increase in complexity, so that in transverse section the contour much resembles the uneven outline of the mucous coat of an alimentary organ (Pl. XXIII. fig. 4), though the folds are less elaborate than those shown by Stieda in the turbot.* Meanwhile the two lateral apertures in the lobi inferiores have descended, so that the inner or infero-median wall touches the folded central chamber. Their central area contains cells in a streaked matrix of protoplasm or coagulable substance. The folded mid-region is somewhat triangular in outline, and continues to increase in size, while the lateral apertures gradually diminish, for the cells soon cover the entire area. After the disappearance of the lateral apertures, the infundibulum becomes more elongated transversely, so as to resemble ultimately a transverse bar, and then it disappears.

About the region of the splitting of the infundibular tissue, and before the crura separate therefrom, the cerebellum appears under the median folds of the optic lobes. It has dorsally the aforesaid lobes, and ventrally the fourth ventricle.

The organ is marked dorsally and ventrally by a median depression, so that from the first it is bi-lobed, and this condition is soon better marked by the occurrence of a median fissure. It diminishes and disappears posteriorly above the point where the pharyngeal teeth occur in the section.

When the tip of the cerebellum (valvula) first appears in transverse section below the tecti lobi optici, the massive area beneath has the two cellular differentiations just below the middle, and the trifid fissure of the infundibulum inferiorly. An intimate decussation of fibres takes place in the lower half, transversely as well as vertically (Pl. XXIII. fig. 6), in the larval fish of 20th June, while the upper half is split by a median furrow, the edges of which, however, are closely attached. Then signs of separation occur between the upper and the lower divisions, a mass of strong transverse fibres passing below the former, and curving upwards at the sides externally. They close the median furrow superiorly, having beneath them in the same region a mass of grey matter. These commissural fibres increase in bulk as we proceed posteriorly, only a median notch existing in the floor above. This continues backward to the medullary region.

Shortly after the anterior fold (valvula) of the cerebellum has become distinctly double, a strong band of transverse fibres passes over the roof of the ventricle to the lateral regions. They proceed on each side to the region of the tori, spreading out into the grey matter. After an interval, in which a change in the vault has occurred, for the tecti lobi optici have now become lateral in the sections, while the median line is occupied by the cerebellum and valvula, another strong band of fibres passes across the same region, the direction in the lateral region being chiefly downwards.

In the cerebellum behind this, various curved fibres cross and vertical bands course from above downward. Towards the termination of the organ a median fissure occurs. Moreover, a bridge of nerve-tissue is thrown over the floor of the ventricle from side to

* *Zeitsch. f. w. Zool.*, Bd. xviii. p. 44, Taf. ii. f. 30.

side, and probably represents the commissure between the lobi posteriores, though these are not conspicuous.

The median fissure of the medulla is at first dorsal and very large, but as the organ diminishes it assumes a lower as well as more central position, and becomes much smaller.

Spinal Cord and Lateral Line.—In the extreme caudal region the posterior (dorsal) fissure of the cord, especially well seen in the wrasse, $\frac{7}{16}$ inch long, is reduced to a mere central canal, circular in transverse section, and surrounded by vesicular matter; indeed the white matter almost wholly ceases, and the column continues to its termination as a ganglionic tube, whose diameter is about one-quarter that of the notochord. This predominance of the grey matter in the hind part of the spinal cord is a character familiar in higher forms.

About the level of the notochord in the cod, $\frac{5}{8}$ inch in length, a canal internal to the corium passes along the outer edge of the septum, dividing the two median lateral muscular masses in the caudal trunk. It is of small diameter, though very distinctly marked on account of the presence of a sheath of black pigment, which continues into the intermuscular septa, and indicates the course of the delicate nervous strand connecting the canal, no doubt, with the spinal cord. Such connection cannot, however, be clearly made out, as the pigment passes only a short distance inward towards the cord. It is to be noted that the spinal cord has similar dark pigment in its protective tunic. The preparations do not show serial openings to the exterior at this stage, and the lumen of the canal is filled with loosely aggregated deeply-stained cells. In *Labrus*, $\frac{7}{16}$ inch long, a canal cannot be made out in the caudal trunk; but an aggregation of cells occurs beneath the integument, on a level with the lower border of the vertebral column. They lie below the pigment-layer of the skin, which stains deeply, and show evidence of nervous connection with the spinal cord. The cells are large and folded, their walls being pushed in—in the form of a figure 8. No lumen in this instance can be discerned.

Ear.—The general form of the ear of the wolf-fish on hatching is shown on Pl. XX. figs. 2 and 4, and on Pl. XXI. figs. 1 and 4. Cartilage develops much more rapidly in the salmon than in the wolf-fish in the otocystic region. Thus, in cutting the ear, both anteriorly and posteriorly, several sections show a complete investment of cartilage in the salmon; whereas at a similar stage in the wolf-fish the thin cartilaginous floor goes only a short distance upward externally, and at no part is a ring of cartilage completely formed. The inner margin of the cartilaginous floor of the ear bends downward posteriorly, and continues into the parachordals, which lie on each side of the notochord. Shortly behind this it also joins the hyomandibular cartilage, passing towards the middle line and disappearing. The general arrangement of the ear is similar in both species, though at no period does the inner border of the capsule pass so near the middle line in the wolf-fish as in the salmon. This is clearly seen in the neighbourhood of the notochord. The structure of the nervous cushions and their auditory cilia or stiff protoplasmic processes in the anterior and posterior chambers present no feature of note.

The properties of the fluid of the chambers are quite adequate for the development of the otoliths toward the internal wall. It is sufficient to point to the growth of the Nemertean stylets to prove how perfectly such organs can be produced in successive generations of the species.

On 20th February a considerable increase in the otocystic cartilage of the wolf-fish had taken place. From before backward this is marked superiorly by an increase in the cartilage behind and above the eye, and inferiorly by a thickening of the bar behind. The great development of the cartilage of the basilar plate around the anterior end of the notochord gives this inferior bar a more distinctly horizontal position, one of its chief flexures being caused, indeed, by the carotid.

On 16th March the cartilaginous mass anteriorly and superiorly has increased so much that it presents a complete ring in section, and thus somewhat further back the cartilaginous boundary is complete externally, while internally it ends abruptly opposite the lower border of the optic lobe. It then sinks downward and presents a large perforated median prominence below the ganglionic mass of the fifth, by which the auditory nerve passes into the cavity. The latter contains large ganglion-cells and hyaline coagulable lymph. After this swelling the cartilage diminishes internally, and ends on each side of a median mass of connective tissue below the infundibulum. Beneath its termination is a space and then an artery and vein (carotid and jugular). The pointed end of the notochord begins above this median band of connective tissue. By and by the cartilaginous floor, now somewhat thin, glides in towards the notochord, and almost coalesces superiorly. At this part it forms a thin wall externally, and ends in a thickened region about half-way up, and the latter increases from before backward over the posterior semicircular canal, until a complete ring is formed round it, only a slender bar connecting the latter inferiorly with the somewhat thickened end at the notochord. The contrast also between the massive inner wall of the canal and the thin outer wall is marked. Then (proceeding backward) the ring is broken internally, and only a slender line externally connects the thickened superior loop with the thin horizontal bar leading to the notochord. The superior mass diminishes and disappears, and the outer part of the horizontal bar becomes disconnected from the denser region at the side of the notochord, the posterior boundary of the ear being formed by a thickened mass of cartilage joined to the arch over the spinal cord, and again forming a ring, as in front, before terminating.

A month later considerable change had occurred in the otocyst—the chief feature being the diminution of the cartilage, which is now covered by a layer of hyaline ossific tissue, running from the notochord over the floor, and along the thin layer of cartilage externally, but the thickened mass to which the hyomandibular is joined does not show it distinctly. As soon as the bar becomes nearly horizontal (sloping a little upward and outward from the cord), this hyaline coat extends from the cord to the upper and outer border of the ear. The three semicircular canals seem to be similar to those in the previous stage, but the ganglionic aperture in the floor anteriorly is less distinct, and the ganglion lies more completely in it. The head of the hyomandibular is rounded, and the cartila-

ginous support of the ear is thinner and more shapely. Membranous lamellæ divide the ear into the three spaces; the external chamber is covered by cartilage, and the posterior follows in the same manner as before. The large otolith lies at the inner and inferior angle near the notochord.

A month subsequently the most noteworthy alteration is an increase in the amount and brittleness of the hyaline coating on the cartilage, and the same may be said for the succeeding month (June), fracture of the supporting skeleton of the ear frequently taking place in sections. The cartilage has diminished as a whole, its cells have become finer, and the brittle hyaline layer has increased in bulk. One of the most brittle regions is the inferior wall of the cavity lying to the inner border of the hyomandibular articulation.

Olfactory Organ.—The chief point examined in connection with this organ was the formation of the two nasal apertures. In the earlier stages the single nasal slit assumed a vertical position, and at the beginning of April was of large dimensions. About the 6th of the latter month a slight promontory was noticed in the middle of each lip of the fissure, and in ten days the promontories had met so as to make an aperture on each side. Each aperture on the 1st May was surrounded by an elevated rim, and the bridge had now become broad. At first the nasal slits lie in a hollow between the eyes, but at the latter date the snout projects further forward. The usual irregularities were observed in a series of specimens, some having the single slit on 21st May and with a considerable yolk-sac, others with the apertures fully formed—as just described.

In *Pleuronectes flesus*, $\frac{5}{12}$ inch in length, the olfactory lobes are somewhat distant from the terminal sac, and the olfactory nerves pursue a course, parallel to each other, between the posterior process of the rostral cartilage and the trabeculæ. On the floor of the cranium the two nerves rest upon a loose connective meshwork, and further back they bend inward, to unite with the olfactory lobes at the point where the superior and inferior oblique muscles of the eye have their origin on the cornu trabeculæ.

A promontory on each lip of the nasal aperture has been already described in the goby, $\frac{11}{24}$ inch long, large loosely aggregated cells forming an outgrowth from the radially disposed cells of the olfactory epithelium (see p. 910). In the post-larval wrasse, $\frac{7}{16}$ inch in length, the transverse septum is complete, and the anterior and posterior nares are now distinctly separated.

Sensory Organs in the Snout.—Remarkable sensory organs occur on the snout of the embryonic haddock (Pl. XXI. fig. 7), and are developed on the maxillary and mandibular elements in the post-larval gurnard. When the latter has reached the length of $\frac{5}{12}$ of an inch, sections of the maxillary bar show organs like the sensory cushions in the otocyst or the papillæ along the dorsal and lateral surfaces of the trunk. The maxilla in section has the form of a flattened plate of hard hyaline tissue placed obliquely. This oblique bar gives off an upper arch, which bends over to meet a short crest sent up from the ventral margin of the bar. A rude tube, very angular in transverse section, is thus formed, but its outer wall is completed only at intervals. In the tube are seated certain sacs, on one side of which a cushion of columnar epithelium

is placed. Sensory hairs appear to occur on the surface of this cushion. Similar sensory organs also occur in a tube hollowed out in the mandibular cartilage. These sensory organs communicate with the exterior, since the tube in which each is placed is in its posterior part incomplete below, and the columnar epithelium on the roof of the cavity is directly exposed to the surrounding medium and to stimuli from the outside.

Alimentary System.—The mouth in the larval *Anarrhichas* presents a different shape from that of the salmon, and on emergence from the egg it is moreover widely open, forming a lozenge-shaped aperture when viewed from the front, and its border is rigid and motionless. Its upper angle (the premaxillary elements) is considerably elevated dorsally, and is depressed between the very large eyes. In this form and in the salmon a peculiar flapping of a process is observed in respiration, and in sections of both species an extension of the mucous membrane of the mouth hangs down and projects inward from the jaws on each side of the trabeculæ (Pl. XXIII. fig. 3, *flm*). This membrane forms a complete floor in front, but posteriorly it runs into lateral flaps, which become continuous with the mandibular articular process. In *Anarrhichas* the smooth fold of this flap posteriorly, as its free tip bends in to join the upper surface, indicates a definite differentiation. In the young salmon the membranous process waves synchronously with the movement of the mandible. The anterior margin of the mouth, in transverse section, forms at first a well-marked groove with the lumen of a vessel in each mandibular elevation. It is to the latter that the soft tissues of the mandible are soon attached. The mucous lining of the roof of the mouth, from the point of junction of the mandible, is comparatively thin, the cells being chiefly of the tesselated variety.

In *Cottus*, $\frac{3}{8}$ inch long, the oral mucous membrane shows large glandular cells, spherical in form, and disposed along the numerous rugæ which are better developed in *Callionymus*. In this last-named species, when $\frac{1}{3}$ inch in length, the mucous layer is very thick and the rugæ most marked. A great increase of glandular epithelium may occur in the lining of the branchial region, and in *Labrus*, $\frac{7}{16}$ inch long, it forms a layer of some thickness at the upper angle of the opercular flap. The mucous coat becomes thicker, and shows columnar cells in *Anarrhichas*, when the notochord appears in section, and the submucous connective tissue increases in volume, so that the internal lining is readily thrown into frills. Outside the sub-mucous coat is a layer of circular muscular fibres. The frills of the mucous membrane are rendered more prominent by the grasp of the increasing circular coat, and the canal is diminished in calibre, so that it forms a comparatively small tube (Pl. XXVII. fig. 6). The columnar and finely granular epithelial lining also has considerably increased in thickness.

In the post-larval Gadoid, $\frac{5}{8}$ inch in length, the general structure of the œsophageal wall is similar, but the grooves in the roof of the pharynx are deep—two ridges projecting very prominently—while on the floor three or more ridges occur. The epithelial coat passes into the grooves, and is very largely developed—the bulky mucous cells resting upon a loose meshwork of connective tissue, with apparently some longitudinal muscular elements. A little further back glands become more abundant, and an outer tunic of

circular fibres appears. This portion of the alimentary canal lies in a spacious recess in the liver, and two lateral hepatic masses abut upon, but do not actually arch over it. In the post-larval wrasse a similar relation of the canal and the liver is noted. The prominent wrinkles of the gut in *Anarrhichas* disappear about the region of the pectoral fins, the canal forming a rounded thick-walled tube with one or two triangular folds. After passing the yolk-sac the canal is larger than in front, and transversely elongated in section, the mesenterial band fixing it to the roof of the abdominal cavity, though it is free elsewhere. Its contour is, however, broken superiorly by the wall of the large portal vessel. A comparatively smooth portion of the gut follows, but folds again make their appearance, in the form of five or six prominent rugæ in section. The mesentery dorsally is thickened, and is almost divided into two portions by a constriction—an upper rounded band, and a lower—which is thinned off superiorly. The rugæ now diminish, the mesentery disappears, and the urinary vesicle takes its place, while the anus opens externally. Proceeding backward, the epithelium of the gut is found to become finer and larger; indeed, in section, posteriorly, it resembles that so characteristic of the alimentary wall in the Annelida; then the folds reappear towards the rectum, and show a somewhat radial striation.

The alimentary canal in the young salmon differs considerably from the foregoing in the region just behind the branchiæ, since it forms a lax tube in transverse section, with thin walls greatly flattened from above downward. The wall increases in thickness in the region of the pectoral fins, and the circular coat assumes larger dimensions, so that the canal is less flattened. It is comparatively small for the size of the fish, the lumen being really smaller than that of the aorta. Towards the posterior part of the pectorals the gut is even less than in front of them. The epithelial (mucous) layer then begins to increase, and a folded condition of the gut causes two layers to appear in transverse section, a smaller superior and a larger inferior. In front of the liver the small calibre of the epithelial coat is in contrast with the thick circular (glandular) layer outside. In the hepatic region the lumen of the gut greatly enlarges, though it is still proportionally less than in the wolf-fish. Behind the liver it slightly diminishes in diameter, and again somewhat enlarges, before assuming the rounded condition characteristic of the rectum, the calibre of which is also smaller. The folds of the gut are much less prominent than in the wolf-fish; and the inner surface of the large cylindrical cellular layer of the rectum is almost smooth. Some of these features, however, may partly be due to the state of the preparations. In the newly-hatched and living salmon, again, the alimentary canal appears between the yolk-sac and the anus as a greenish band. About the tenth day distinct transverse markings are observed in the tract, two especially conspicuous above the origin of the ventral fin. Between the fourth and fifth weeks, the functional activity of the alimentary canal is considerable, and numerous fæcal masses occur in the rectum. The teeth are now evident in both upper and lower jaws. A little later food of various kinds is found in the stomach and intestine. The pyloric cæca on the nineteenth day form mere conical elevations on the duodenum, and have the aspect of short papillæ of a cellulo-granular nature. It is remarkable that the pancreas (assuming the cæca to represent it)

should have an origin so different in the higher animals. However, the condition of that organ in the sturgeon, tunny, and other forms would lend colour to such a view, even with the knowledge of the special rudiment in such forms as *Salmo*, *Perca*, and *Platessa*.

Towards the end of February, and later, many of the larval wolf-fishes showed a whitish streak in the interior of the intestine. It was uniformly opaque white, and apparently consisted of nutrient matter. In section this mass presented a series of peculiar crystalline and probably fatty bodies.

The changes which take place in the structure of the digestive tract in *Anarrhichas* are noteworthy, and consist chiefly of the differentiation of the elements of the mucous lining, the increase of the circular and longitudinal muscular fibres, and the greater complexity of the folds of the walls, chiefly internally, but also externally. In the stage just described (17th January) the stomachal part of the canal has attained little development, and its mucous coat shows only a few frills of finely granular epithelium. As development proceeds, however, the œsophageal region of the canal is thrown into a complex series of frills, and the mucous lining is supplied with large globular glands. In the oldest stage (20th June) the folds of the œsophageal region are more complex than in the earlier stages, many of them being subdivided, and the longitudinal fibres (inside the circular) are more distinct dorsally and ventrally. The glands are arranged as a close and somewhat regular series of globular bodies along the inner surface of the folds (Pl. XXVII. fig. 5). Proceeding backward the complexity of the folds increases, while the canal becomes rounder, the lamellæ being pinnate in transverse section, from the number of the secondary folds. The globular glands now cease in the walls of the folded ridges, and an alteration occurs in the appearance of the latter, which assume a more or less circular condition in section, and in their wide bases are a series of large circular areolæ,* probably glandular (*dre*, Pl. XXVII. fig. 4), the inner wall of the gut over these being composed of closely-set cylindrical epithelial cells. These globular spaces also occur under the wall, where there are no lamellæ. The calibre of the canal becomes smaller and the lamellæ thicker, a few secondary processes or folds appearing on their surface. The latter has fine columnar epithelium, and the submucous tissue is composed of granular glands, probably modifications of the large areolæ in front. These lamellæ become more distinctly pinnate before ceasing at the pylorus. The wall of the canal is highly muscular, the fibres forming a complexly interwoven layer externally. The next region of the canal to be distinguished is that behind the valvular folds of the former, and it is characterised by its thinner muscular walls, and the change in its glandular lining, for the numerous simple folds around its walls have coarser and more lax epithelium than the foregoing. Externally is a peritoneal investment (with probably a few muscular fibres), then longitudinal fibres grasped between the outer and the next layer, with, finally, an internal circular layer of fibres.

Posteriorly, the gut diminishes in calibre, and by and by the folds chiefly affect the

* These areolæ in the sketch are perhaps too conspicuously cellular.

upper wall. Certain parts of the rectum, on the other hand, are most complexly folded (Pl. XXV. figs. 3, 4, 5, and 7), only a central area in the sections being devoid of rugæ. The folds continue until the external aperture is reached (fig. 5).

In the embryo of the salmon, forty days after fertilisation, the alimentary canal is closed in the cardiac region, and remains of small calibre throughout the rest of its extent; indeed, at the commencement of the segmental ducts, it is less in section than the notochord, and is very little larger than one of the segmental ducts. When thirteen days old, the alimentary canal in the region of the heart is more or less median in position, and presents two lateral slits. It then opens out, and again contracts to a small tube less than the girth of the notochord in the region of the liver, its epithelial coat forming a simple lining, without rugæ. The tube, for the most part, remains simple to the posterior termination.

The young salmon, forty-five days old, artificially reared, has its œsophageal region less developed as regards size, and the mucous rugæ internally. The globular glands, however, have a similar arrangement, though they are proportionally larger. The basement-tissue is coarsely granular. The circular muscular coat is strongly developed. The canal is peculiar on account of the rapid narrowing that takes place, and the disappearance of the globular glands, the section of the entire canal in this region being only a little larger than that of the notochord.

In the Gadoids and Pleuronectids the structure of the alimentary canal agrees in the main with the features seen in *Anarrhichas*—the œsophageal portion, of small calibre, having thick walls with complex internal ridges, while posteriorly the walls become thinner and saccular, the internal ridges much less prominent, and the diameter of the canal greatly increased. In *Callionymus*, $\frac{1}{3}$ inch long, the mucous membrane of the oral cavity rises into very thick prominences or longitudinal folds, which are richly glandular.

Swim-Bladder.—In many post-larval fishes the swim-bladder retains, until a comparatively late stage, its embryonic character as a sac lined by a thick layer of large soft epithelial cells, often so well developed anteriorly as to reduce the lumen of the organ to that of a narrow tube. In the cod, $\frac{9}{24}$ inch in length, this is the condition, and the anterior portion is traversed by a large hæmal trunk. The capacity of the bladder at a later stage enormously increases, and when the young Gadoid reaches the length of $\frac{5}{8}$ inch, this structure has thin membranous walls with a layer of thickened epithelium only on the inner surface. In the post-larval Clupeoid, $\frac{5}{12}$ inch long, it is large, and has a similar structure to that just described in the Gadoid, with, however, a less marked development of the epithelial coat. The epithelium of the inner surface in *Callionymus*, $\frac{1}{3}$ inch in length, rises into thick massive folds; but the most remarkable development of this layer in the swim-bladder is seen in the gurnard, $\frac{1}{4}$ inch long, the large pulpy cells, each with its nucleus placed excentrically nearest the free surface, forming thick rugæ, and supported by a layer of smaller cells irregularly scattered as an outer tunic. The large epithelial cells just described also occur in the swim-bladder of the Gadoid, when $\frac{1}{2}$ inch in length, and the deeply-stained nucleus is excentric in position; but it

is most distant from the free edge of the cell. In the later post-larval stages of the gurnard further changes occur, the deep glandular epithelium of the anterior part of the swim-bladder enclosing a narrow lumen. A little further back the thick glandular epithelium is continued into a lateral blastema of deeply stained tissue on each side. The cells are, however, altered in form, being spherical with a definite nucleus, and the cell-contents are now clear. The lumen of the bladder becomes posteriorly narrowed in the form of a neck, and pulpy globular cells, with deeply stained (glandular ?) contents take the place of the cubical epithelial cells of the fore part of the sac. These rounded cells form a superficially broad girdle. Behind the narrow neck the bladder expands again, but its walls are thinner and the layers distinguishable are fewer. Thus, in the anterior part, outside the greatly thickened mucous lining, a dense nucleated stratum occurs, which rests upon a striated fibrous layer, bounded externally by a very thin nucleated stratum—the nuclei being much flattened and elongated, and lying two or three deep. An outer tunic of thick connective-tissue circumscribes the bladder, and this rests in the anterior part upon the pigmented peritoneum. Posteriorly, the liver and intestine are in contact with the external connective tunic. The four layers just described, with the exception of the deep internal mucous layer, continue into the second part of the bladder, but are much thinner. The great bulk of the liver and the pronephric augmentation are probably influential in the shifting backward of the swim-bladder. As shown in the earlier part of this paper, the swim-bladder is a protrusion from the embryonic œsophagus; but the lengthening of the gullet, the enlargement of the stomach and intestine, produce such changes in the disposition of the abdominal viscera as greatly to disturb the primitive relations of the various organs. Professor Cleland, in a valuable note* points out that the origin of the swim-bladder as a thoracic evagination must determine the regions of the alimentary tract (*e.g.*, pharynx, stomach, and intestine); but it has to be borne in mind that, when the evagination takes place, the tract is very short, and the cystic duct is pushed out of the ventral wall in such close proximity to the outgrowth of the swim-bladder as to be included in the same section of the embryo, if cut in a slightly oblique plane,—the duodenum and pharynx in the early stage being separated by a very short interval. It is possible, therefore, that in the elongation and differentiation of the parts of the alimentary canal, the point of origin for the swim-bladder may, in post-larval and still more in adult stages of different species, be found in parts which do not perform the same physiological function. The position stated by Professor Cleland is not, however, affected by this consideration, and the part called stomach in such a form as *Clupea* must be morphologically—if not functionally—pharyngeal.

Liver.—The liver in *Anarrhichas* appears on both sides of the fish posteriorly, but in the salmon it is best seen on the right side. Consequently the arrangement of the blood-vessels which pass through it for the supply of the yolk-mass diverge considerably in the two species. The position of the liver is seen in the outlines of the right and left sides (Pl. XX. figs. 2 and 4).

* *Memoirs in Anatomy*, 1889.

In the young Pleuronectid, $\frac{9}{24}$ inch long, the liver is of considerable size, and fills up the main part of the large peritoneal cavity in front. This chamber is very capacious, and causes the abdomen to hang like a swollen sac on the ventral side of the young fish. Its walls are thin, a delicate sheet of muscle merely intervening between the integument and the internal peritoneal lining. Posteriorly the spacious intestine fills up the cavity. Anteriorly the narrow œsophagus passes above the liver; but in many forms it descends into the hepatic mass—so deeply in the salmon and in the wrasse $\frac{7}{16}$ inch long as to be almost enveloped by the liver, as we see in a less degree in the Gadoid when $\frac{5}{8}$ inch in length.

The gall-bladder forms a large rounded diverticulum in the midst of the liver on the right side. The outer layer is fibrous and probably muscular, while the inner consists of flattened, epithelial cells. At this stage two apertures are visible, one leading from the anterior division of the liver by a somewhat convoluted duct, the other entering the bladder towards its posterior border on the same side, *i.e.*, the left.

Spleen.—In the gurnard, $\frac{1}{4}$ inch long, and skulpin, $\frac{1}{3}$ inch long, a rounded body occurs behind the liver. It is sheathed in a delicate cellular wall, and is formed of cells which stain deeply, grouped together in clumps, and forming a fairly solid organ. In *Cottus scorpius*, $\frac{3}{8}$ inch long, an organ of similar histological structure passes along the posterior dorsal surface of the liver. No limiting membrane separates it from the liver, but its cells stain more deeply than those of the hepatic mass. Its form is flattened and lobular, with blood-corpuscles filling up its interstices, and it is apparently the spleen.

Branchial System.—On the first day the branchiæ of the salmon have simple rows of papillæ, each with a loop formed by a blood-vessel. On the second or third day, probably somewhat earlier, the operculum is noticed to flap actively, and a single series of blood-corpuscles rush up one side and down the other side of the branchial fimbriæ. Small-celled cartilage is present in the branchiæ on the eighth day, and respiration is active, while on the fourteenth day, the embryo respires 106 to 108 times per minute. On the nineteenth day (sixth to seventh week after fertilisation) the branchial fimbriæ are proportionately large and blunt.

In the wolf-fish each branchial arch, on the 16th January, presents externally the cuticular investment, then a dense cellular layer (hypoderm) of connective and glandular tissue, this being greatly thickened on the margin, which afterwards becomes laminated. The cartilages of the arch have in transverse section a thick marginal structureless ring and a cellular centre. The papillose processes in *Anarrhichas*, on the thickened edge, increase in size in February, but they do not show much further differentiation during this month. In March the branchial papillæ are simple, and their vascularity is evident towards the end of the month, a large loop occurring in each. In April the elongated process becomes pinnate, a feature still more evident in May, so that each is feather-like, after the plan of those figured in the very young flounder (Pl. XV. fig. 8). Little further change ensued in those examined in June.

The arrangement of the hyoidean apparatus and of the branchial arches, in fairly developed forms, is shown in Pl. XXV. figs. 1 and 2.

The hyaline investment of the branchial arch described in the early larval *Anarrhichas* appears first in the post-larval Gadoid, $\frac{5}{18}$ inch in length. It clothes the cartilaginous branchial arches and the hyomandibular element as a very thin perichondrial layer, which develops very strong blade-like ridges at a later stage (when the fish measures $\frac{5}{8}$ inch in length). These ridges are three in number, one directed dorsally, the other two ventrally, and enclosing an angle in which the branchial vein passes. The central core of cartilage appears to be rapidly diminishing in diameter, and the hyaline investment is very thick. The branchial pinnæ now form a double row along the artery of each arch, and they consist simply of folds of mucous membrane, the cells being very large and defined by a thin external membrane. Delicate cartilaginous supports appear as thin rods projecting from the arch, but not, however, as outgrowths from it. In the post-larval gurnard, $\frac{5}{12}$ inch in length, these features are well marked, and in *Cottus scorpius*, $\frac{5}{8}$ inch in length, the details are even more readily made out; the hyaline deposit is not very thick, nor does it show any indication of the ridges described above. Outside the hyaline layer clothing the cartilaginous arch is an investing connective-tissue stratum in which the arterial and venous trunks lie. It appears to include some muscular elements. An epithelial layer lies externally, and it is much thickened on the anterior or upper side of the arch. Numerous large cells (mucous?) and vesicles occur in it, and it forms the complex folds of the pinnæ. In this form (*Cottus*) the cartilaginous rod developed in each pinna is very definite. In the gurnard, $\frac{5}{12}$ inch in length, two muscles pass along a part of the first branchial arch on its ventral side, to be inserted on the copula (basibranchial) of that arch. Before reaching the point of insertion the two muscles lie close together, and in the interval an upright plate of hard hyaline tissue is deposited; anteriorly it sends out two horizontal plates from its ventral margin, and has in transverse section the form of an inverted T. The branchial artery is very well developed at this stage, having a dense external tunic, within which is a thick fibrous and muscular layer, with longitudinal fibres in separate bundles internally; these cause ridges in the epithelial lining, and in transverse section they project boldly into the lumen of the vessel. In oblique sections along the branchial arches of a post-larval Gadoid, $\frac{11}{24}$ inch in length, it is observed that the pinnæ of one side of the arch are not placed opposite those of the other side, but alternately, each with the central cartilaginous support described above.

Renal Organs.—Just behind the point where the notochord commences, and below the large basilar plate in the larval *Anarrhichas* of 17th January, cellular glands appear in the space between the parachordals and the roof of the pharynx. The glandular body on each side shows certain empty spaces around it, and lies beneath the auditory vesicle. It is composed of rather large nucleated cells, the whole having at first in vertical transverse section an ovoid outline and a thin hyaline investment. The jugular vein lies to the inner side of each, in the connective tissue which fills up the interval between the

cranium and the pharyngeal roof below. Further back these glandular organs enlarge, and, as two preparations seem to show, they become lobulated, while the vessel on the inner side is surrounded by large nucleated cells. Pigment-corpuscles, moreover, appear at the side of the apertures and near the aorta. Toward the posterior border of the cranium, where a short conical spur abuts on the notochord on each side, the renal organ proper, or pronephros, commences in the form of numerous coils of the segmental duct (Pl. XXIII. fig. 2, *prn*); moreover, shortly behind, in the middle line below the aorta, two symmetrical spaces occur, into each of which a round vascular mass (glomerulus) having a glandular appearance, projects, the outer side of each aperture being free (Pl. XXVI. fig. 4, *gl.*). The pigment-corpuscles greatly increase, the main mass being situated dorsally over the segmental ducts, but also between and below them. Besides the ducts a quantity of glandular tissue (apparently Balfour and Parker's lymphatic tissue) occurs at the inner and inferior border of the region. The coils of the segmental duct form a considerable mass as they pass backward, but they soon diminish. The course of each, laterally, varies in those species of Teleosteans in which a swim-bladder is developed, the large capacity of this median structure causing the ducts to be widely separated anteriorly. In the post-larval cod, $\frac{1}{2}$ inch long, they pass along the side of the swim-bladder by a gently descending course to the urinary bladder. The increase in the cellular matter (which stains deeply) surrounding the tubules of the pronephros is very marked in the post-larval stages, and in the young gurnard, $\frac{1}{4}$ inch long, it forms quite a large lobate mass enclosed in a very delicate membrane or capsule, the two glomeruli being imbedded in this apparently glandular matrix. A similar development of these small cells, which stain deeply, is seen in the cod when $\frac{5}{18}$ of an inch in length, and much dense pigment is developed around the pronephros. The ducts, when traced backward at this stage, pass in the wolf-fish over the urinary bladder, and posteriorly curve round, and debouch into the bladder by a very sharp downward deflection. By and by only a single duct remains with a connective-tissue investment, in which pigment-corpuscles occur all round, except at the inner and inferior border. Subsequently a small solid mass of nucleated cells is seen at the inner and inferior border of the duct; but no definite structure can be made out, and it soon comes to an end, to be succeeded by similar bands often passing toward the opposite duct. Moreover, in some sections a tubular structure indicates that these are probably segmental tubes in an early condition. These sections are, however, situated high up—close by the sides of the aorta, but they do not appear to connect with it, and they have lax cellular walls. Soon the cardinal vein becomes single, and frequently the cells referred to form a thin band over it. Posteriorly the segmental ducts seem to diminish rather than increase in size, and the large cardinal vein widely separates them. By the diminution of the cardinal (caudal) vein the ducts again approach, and the space between the notochord and the rectum increases by the downward curve of the latter, while the fold of peritoneal mesentery, suspending the gut, disappears. The segmental ducts also move further from the notochord, and their lower ends merge into a dilated common part—the urinary vesicle—

the wall of which superiorly appears to be composed of cylindrical epithelium with a fibrous outer investment passing into the connective tissue surrounding it (Pl. XXV. fig. 5).

The glomerulus on 1st March presents a more distinctly looped arrangement (Pl. XXVI. fig. 4), the basal regions being narrow and closely applied to each other, the free portion having a pear-shaped outline, and in transverse section showing long spaces, so that it has a somewhat looped appearance. These chambers above are formed by thin membranous walls studded over with small globular cells. The anterior cardinal veins, as they debouch into the venous sinus, are outside the glomerulus and the pronephros. On 16th March the cellular stroma towards the posterior part of the segmental ducts increases superiorly on the sides of the cardinal veins, and above the ducts. It soon forms two symmetrical masses above the latter, the constituent cells of which are arranged somewhat in rows, so that there is a tendency to a tubular structure. A series of vascular spaces, however, develop at the commencement of the urinary vesicle, and the tissue disappears. The preparations of 20th April distinctly show in this region segmental tubes on a miniature scale.

These secondary growths, moreover, have extended much further forward. It is remarkable that, though the cellular tissue has greatly increased anteriorly, and for some distance backwards, no distinct tubes appear there at this date.

On 1st May the chief change is the increase of pigment round the pronephros, which has a proportionally large bulk—the two sides forming on section an area equal to that of the alimentary canal. In the glomerulus nothing new is observed. A large vein runs down the right pronephros towards its termination, and then bends to the middle line. The segmental duct is now reduced to a single canal on each side, and, having reached the middle line beneath the aorta, the masses of cells superiorly, that is overlying the ducts, become more complex, and segmental tubes branch out—occurring both above and below the aorta, and beneath the cardinal vein in the middle line. The segmental ducts increase in size as the tubes become numerous, and each, like the ducts, has a hyaline investment (Pl. XXVI. fig. 3). A granular substance occupies the centre of the segmental duct in section (Pl. XXV. figs. 4, 5, 6, and 7).

The mass of cells, above described in *Anarrhichas*, is late in appearing in most of the other forms studied. In *Labrus*, $\frac{7}{16}$ inch long, it forms a thick cylindrical column, over the two segmental ducts in the terminal part of their course.

The intimate relation of the pronephros and the posterior cranial nerves is remarkable, the large cellular outgrowths of the brain, which mark the egress of the ninth and tenth nerves, are closely associated with the cellular stroma of the head-kidney, and the similarity, in the early condition, of the nervous and renal tissue is striking, especially at such a post-larval stage as that of the gurnard, when $\frac{5}{12}$ of an inch long. The roots of the glosso-pharyngeal and vagus exhibit enormously enlarged ganglionic swellings in the example just instanced. The head-kidney, moreover, becomes so greatly increased in bulk dorso-ventrally as to extend in the cod, $\frac{5}{8}$ inch in length—from the roof of the body-cavity almost to the level of the summit of the neural arch.

The urinary vesicle presents a series of boldly marked folds superiorly, and its walls are in contrast with the massive sheath of the rectum. The segmental tubes are thus not developed in the pronephros, but have advanced considerably forward from the metanephros. In the pronephros the coils of the duct amidst the cellular mass seem to take the place of the tubes behind. Like the interior of the chamber, the duct leaving the urinary vesicle (Pl. XXV. fig. 6) is lined with columnar epithelium, and it opens on a special papilla. The differences between the anterior region of the urinary vesicle before and after the development of the segmental tubes is clearly shown by contrasting figs. 5 and 7 of Pl. XXV. The development of the pigment on the wall of the organ (urinary vesicle) is also a noteworthy feature.

Body-Cavity.—The form and capacity of this chamber varies very much in post-larval stages. It may constitute, as pointed out on a prior page, a huge depending sac, especially well seen in Pleuronectids. In the flounder, $\frac{9}{24}$ inch long, it is a thin-walled protruding pouch, anteriorly occupied by the bulky liver, while posteriorly the capacious intestine mainly fills up its cavity. Precisely the reverse condition obtains in the post-larval Clupeoid, $\frac{5}{12}$ inch long, the body-cavity appearing merely as a slit-like space between the lengthened intestine and the peritoneum in front, the liver passing beneath the alimentary canal as well as the large swim-bladder behind, and reducing the space very much. In the goby, too, at $\frac{9}{24}$ inch, the body-cavity diminishes posteriorly so much as to form an interval barely perceptible between the intestine and the body-wall. Its anterior end may, as in a Gadoid, $\frac{5}{18}$ inch long, pass beneath the pericardium, so that in section the ventricle of the heart occupies a position superior to the compact fore-end of the liver. This sub-pericardial protrusion of the body-cavity exhibits a thick muscular mass in its wall upon each side. The viscera in the post-larval wolf-fish and salmon appear to fill up the limited peritoneal chamber more completely than in the spacious and prominent cavity characteristic of such forms as the Pleuronectids and the ling.

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LIST OF REFERENCE LETTERS.

a. anus.
abd. abdomen.
ab. air-bladder.
ac. anterior commissure.
af. anal fin.
al. alar expansion of scutum (*bs.*).
ao. aorta.
aob. aortic bulb.
ar. artery.
au. otocyst (early condition).
auc. auditory capsule.
aur. auricle.
b. brain.
bc. body-cavity.
bd. blastodisk (before segmentation).
bdm. ,, (after segmentation).
bl. blastomeres.
blc. blood-corpuscles.
blr. urinary bladder formed by union of segmental ducts.
bp. blastopore.
br. blastodermic rim.
bra. branchial arches.
brc. ,, clefts.
bs. blastodermic shield.
car. carina, or ventral ridge of early embryo.
cart. cartilage.
can. canal (auditory, &c.)
caps. capsule.
caud. caudal end of trunk.
cb. cerebellum.
cdv. caudal vein.
ce. cerebrum, anterior fore-brain.
ceph. cephalic end of embryo.
cf. caudal fin.
ch. choroidal fissure.
cl. clavicle.
cp. cortical protoplasm.
cs. cuticular (hypoblastic) notochordal sheath.
ct. cartilage, and connective tissue.
ctr. cornu trabeculæ.
cv. cardinal vein.
dc. ductus choledochus.
df. dorsal fin.
dg. dorsal or medullary groove.
duc. ductus Cuvieri.
e. eye.
ed. epidermis.
ef. embryonic (marginal) fin.
ep. epiblast.
$ep._2$,, corneous.
$ep._1$,, neurodermal.
er. embryonic fin-rays.
fa. anterior transverse fibres.
fb. fore-brain.
fbr. roof of fore-brain
fg. branchial ruaments.
fG. fornix of Gottsche.
g. gut. *fg.* fore-gut.
mg. mid-gut.
hg. hind-gut or rectum.
b. gall-bladder.
gc. germinal cavity.
gl. glomerulus.
h. heart.
ha. hæmal arch.
hb. hind-brain.
hg. hind-gut.
hm. hyomandibular arch.
hmc. ,, cleft.
hr. rudiment of heart.
hyd. hyoid element.
hyp. (or *hy.*) hypoblast.
i. iter a tertio ad quartum ventriculum.
inf. infundibulum.
inn. interneural (spinous) cartilages.
ir. iris.
iv. subintestinal vein.
k. kidney.
Kv. Kupffer's vesicle.
l. lens.
lr. liver.
ll. lower layer (primary entoderm) cells.
ly. lymphatic mass in front of kidney.
li. lobi inferiores.
m. mouth.
ma. meridional areas of protoplasmic transference.
mb. mid-brain.
mc. permanent medullary canal.
md. and *mo.* medulla oblongata.
me. mesenteron.
mel. membrana elastica externa.
mes. mesoblast.
mg. mid-gut.
mic. micropyle.
mn. mandible.
mro. musculus retractor oris.
msn. mesentery.
mx. maxillary.
my. myotomes, muscular somites, or myomeres.
n. nucleus.
na. neural arch.
nc. notochord.
ncs. notochordal sheath.
ncu. nervous cushion (auditory).
ne. neurochord.
ncc. neurenteric canal.
nic. cellular ring of notochord.
np. nuclei of the periblast.
nv. nerve.
og. oleaginous sphere or globule.
ol. nasal pits.
olf. olfactory lobes.
oln. ,, nerves.
op. optic vesicle, also eye in later stages (*oc.* in some figures).
opc. operculum.
opcm. optic commissure.
opl. ,, lobes.
oto. otoliths.
ovf. valve-like flap of optic lobe
p. protoplasm.
pch. pigmented layer of choroid.
pcs. perichordal (mesoblastic) sheath.
par. parachordals.
pd. pericardial chamber.
per. periblast.
pf. pectoral fin ; also pale commissural fibres.
pg. pectoral girdle.
plp. palpocils.
pn. pineal gland.
pv. primitive germinal cells.
pou. ,, opercular aperture.
pq. or *ptg.* palato-quadrate cartilage.
pr. (also *my.*) protovertebræ.
prc. pronephric chamber.
prs. primitive streak.
prn. pronephros.
prn'. ,, opening into *prc.*
ps. perivitelline space or "breathing chamber."
pt. pituitary body.
ptg. pterygo-quadrate.
pv. portal vein.
pz. parietal zone of blastoderm (resembling the Avian zona pellucida).
quad. quadrate part of mandibular arch.
rb. rib.
sb. swim-bladder.
sg. archinephric or segmental duct.
sgc. segmentation cavity.
sd. segmental tubes.
sno. sensory organs.
so. somatic mesoblast.
sp. splanchnic mesoblast.
sph. spherules.
spn. spinal nerve.
ss. serous spaces around embryo.
st. stomach.
sv. sinus venosus.
th. thalamencephalon or posterior fore-brain.
thl. lobes of roof of thalamencephalon.
thr. floor of thalamencephalic chamber.
tr. trabeculæ.
ts. tori semicirculares.
tl. ,, longitudinales.
uv. urinary vesicle.
v. vesicle.
vn. ventricle (heart).
vf. ventral fins.
vn. vein.
vt ventricle (brain).
vth. vesicle of thalamencephalon.
vs. blood-vessel.
x. variously used for special structures.
y. yolk.
ys. yolk-sac or embryonic membrane.
zr. zona radiata.

I. Olfactory nerve.
II. Optic nerve.
III. Oculo-motor nerve.
VII. Facial and auditory nerves.
V. Trigeminal nerve.

EXPLANATION OF PLATES.

[The Plates were drawn under the impression that they would be published by the Fishery Board for Scotland. This was found to be impracticable. The larger share of the cost of their publication was borne by the Royal Society of Edinburgh, part of the balance being defrayed by a grant from the Fishmongers' Company of London.]

Plate I.

Fig. 1. Ovum of *Liparis montagui*, pinkish in colour and with pitted capsule, . . . × 50
Fig. 2. Ovum of *Cottus bubalis* (?), showing boldly corrugated zona radiata, . . . × 24
Fig. 3. Ovum of *Cottus scorpius*, ... × 24
Fig. 4. Ovum of *Liparis montagui*, with pitted capsule. Adjacent ova are attached by strong facets, ... × 40
Fig. 5. Fertilised ovum of *Clupea sprattus*, ... × 56
Fig. 6. Ovum of *Zeugopterus punctatus*, in ripe (unfertilised) condition, ... × 56
Fig. 7. Fertilised ovum of *Trigla gurnardus*, cells at the edge of the blastoderm, . . . × 90
Fig. 8*a*. *T. gurnardus*, pigment-corpuscles present at the closure of the blastopore, . . . × 205
Fig. 8*b*. „ pigment-corpuscles present at the closure of the blastopore, . . × 205
Fig. 9. Spermatozoa of *Trigla gurnardus*, ... Highly magnified
Fig. 10. Ova of *Molva vulgaris*, floating in calm water, showing a regular disposition. The ring next the central oil-globule indicates the blastoderm, ... × about 10
Fig. 11. *G. æglefinus*, micropyle and accessory structure in oblique view, ... × 415
Fig. 12. „ micropyle in profile, ... × 205
a, external crater; *b*, smaller internal orifice; *c*, conical internal elevation.
Fig. 13. „ micropyle in profile, another view of a later condition in an ovum 4½ hours after fertilisation, ... × 400
Fig. 14. „ micropyle in profile, 6 hours after fertilisation, ... × 500
Fig. 15. „ micropyle and accessory structure, oblique view, ... × 510
[The artist has placed the accessory structure above instead of at the side of the micropyle.]
Fig. 16. *T. gurnardus*, surface view of an abnormal zona radiata, ... × 205
Fig. 17. *a*, *b*, *c*, *d*, and *e*, successive changes observed in the polar nuclear body, apparently the union of male and female pronuclei in the ovum of *T. gurnardus*: *a*, at 25 mins.; *b*, 30 mins.; *c*, 38 mins.; *d*, 46 mins.; *e*, side view of another similar body, . . × 75
Fig. 18. *Pleuronectes microcephalus*, surface view of dotted and reticulated zona radiata, . . × 350
Fig. 19. *Trigla gurnardus*, zona radiata with linear arrangement of dots, ... × 300
Fig. 20. *Pleuronectes platessa*, zona radiata showing dotted structure, ... × 415
Fig. 21. *Liparis montagui*, nearly ripe ovum, with reticulated capsule and oil-globule, . . × 156
Fig. 22. Oblique view of the same.
Fig. 23. *Agonus cataphractus*, reticulated zona radiata, ... × 250
Fig. 24. *Cyclopterus lumpus*, zona with dots of two sizes, ... × 205
Fig. 25. *Anarrhichas lupus*, zona in section, stained with hæmatoxylin, which affects only a thin line *a*, ... × 435
Fig. 26. Ovum of *Solea vulgaris*, viewed from above, so as to show the ring formed by the groups of small oil-globules; the rim of the blastoderm is observed internally, and certain parasitic infusoria are seen externally, July 12, 1888, ... × about 40

Plate II.

Fig. 1. *Pleuronectes flesus*, vertical section through middle of blastoderm, 2nd day, April 7, 1886, × 175
Fig. 2. „ „ vertical section through middle of blastoderm, nearer the margin than in fig. 1, ... × 175

Fig. 3. *Gadus æglefinus*, section through the blastoderm at the morula stage, 22nd hour, March 25, 1886, ... × 175
Fig. 4. „ „ surface view of the edge of the blastoderm and periblast, 26th hour, March 30, 1886, ... × 175
Fig. 4*a*. „ „ surface view of the same, 2 hours later (28th hour), . . . × 175
Fig. 5. *T. gurnardus*, yolk pitted by periblastic nuclei, viewed obliquely from above, . . × 90
Fig. 6. „ periblast and edge of blastoderm, May 26, 1886, ... × 415
Fig. 7. „ similar view, 8th hour, June 25, 1886, ... × 156
Fig. 8. „ similar view, 8th hour, May 26, 1886, ... × 415
Fig. 9. *Gastrosteus spinachia*, part of rim and of blastoderm when extended about nine-tenths over the yolk-surface, ... × 130
Fig. 10. *G. æglefinus*, section through the invaginated rim when almost at the equator, 4th day, and no germinal cavity present, ... × 435
Fig. 11. Ovum of *Solea vulgaris*, showing chromatophores over the yolk and groups of oil-globules segregated under the embryo, ... × 50
Fig. 12. Ovum of *Gastrosteus spinachia* in the morula condition, May 9, 1886 : *x*, facets of attachment to adjacent ova, ... × 25
Fig. 13. Newly-hatched larva of *Clupea sprattus*, ... × 21
Fig. 13*a*. Larva of *Clupea sprattus*, stage (in a somewhat abnormal specimen with minute papillæ behind and below eye, and on the anterior surface of abdomen) more advanced than in the preceding figure, ... × 12
Fig. 14. *T. gurnardus*, May 24, 1886. Three oleaginous spheres were present in this ovum, . × 55
Fig. 15. *a*, *b*, *c*, *d*, *e*, *Pleuronectes flesus*, vertical sections through the blastoderm on the 3rd day, April 7, 1886 : *a*, through the middle of the germ ; *c* through the marginal part, . × 150
Fig. 16. Ovum of *Gadus æglefinus*, marginal blastodermic cells sending out filamentous protrusions under pressure, ... × 230
Fig. 17. *Gadus æglefinus*, vertical section through an ovum with the rim nearly at the equator; no germinal cavity appears, 4th day, March 24, 1885, ... × 64
Fig. 18. Ovum of *Gadus æglefinus*, vertical section through the blastoderm at the 2-cell stage; many vesicles are collected at the base of the blastomere, ... × 435
Fig. 19. Ovum of the haddock on the 3rd day, at 10 A.M., viewed from above, . . . × 30

Plate III.

Fig. 1. *T. gurnardus* of the 3rd day, transverse section through the cephalic region, . . × 175
Fig. 2. „ of the 3rd day, transverse section posterior to fig. 1, . . . × 175
Fig. 3. „ of the 3rd day, transverse section through the terminal portion of trunk (primitive streak ?), ... × 175
Fig. 4. „ of the 9th hour, May 28, 1886, cephalic end of embryo, . . . × 225
Fig. 5. „ of the 3rd day, May 27, 1886, snout of embryo, ... × 250
Fig. 6. *G. æglefinus*, of the 72nd hour, snout of embryo, ... × 250
Fig. 7. „ of the 6th day, March 29, 1886 (Kupffer's vesicle and blastopore), . . × 400
Fig. 8. *G. morrhua*, of April 26, 1886, 10 A.M., end view, ... × 250
Fig. 8*a*. „ of April 26, 1886, somewhat later than fig. 8, end view of early embryo, . × 250
Fig. 8*b*. „ of April 26, 1886, 11.40 A.M., ... × 250
Fig. 8*c*. „ of April 26, 1886, 12.45 noon, ... × 250
Fig. 9. „ of May 1886, side view of blastopore and neurenteric canal, &c., . . × 97
Fig. 10. „ of May 1886, side view of blastopore and neurenteric canal, &c., . . × 97
Fig. 11. *G. æglefinus*, of May 25, 1886, transverse section through the trunk (rim at equator), . × 175
Fig. 12. „ transverse section through the caudal region (primitive streak ?), same stage as fig. 11, ... × 175
Fig. 13. „ of May 26, 1886, transverse section through the trunk (rim past equator), . × 175
Fig. 14. *G. morrhua*, of April 26, 1886, Kupffer's vesicle viewed through the transparent embryo, × 150

Fig. 15. *G. morrhua*, of March 16, 1886, side view of blastopore with a plug of yolk, . . × 97
Fig. 16. *T. gurnardus*, of May 28, 1886, surface view of caudal end of embryo at an early stage, . × 125
Fig. 17. *G. æglefinus*, of March 25, 1886, 4 P.M., similar stage to the preceding figure, . . × 97
Fig. 18. *G. morrhua*, of April 26, 12.30 P.M., side view of caudal end, ... × 205
Fig. 19. „ front view of cephalic end of embryo, with peculiar fold of epiblast and hypoblast, ... × 90
Fig. 20. „ similar view to fig. 18, ... × 90
Fig. 21. „ of May 12, 1886, blastopore closing, ... × 52
Fig. 22. *T. gurnardus*, of May 28, 1886, 4th day, caudal end of embryo viewed laterally, . . × 40
Fig. 23. *G. morrhua*, of May 16, 1886, 90th hour, caudal end of embryo and blastopore viewed from above, ... × 175

PLATE IV.

Fig. 1. Transverse section of embryo of *Pleuronectes flesus*, 4th day (snout), . . . × 200
Fig. 2. „ „ „ „ 4th day (fore-brain), . . . × 200
Fig. 3. „ „ „ „ 4th day (optic vesicles), . . × 200
Fig. 4. „ „ „ „ 4th day (nuchal region), . . × 200
Fig. 5*a*. „ „ „ „ 4th day (posterior region of the trunk), × 200
Fig. 5*b*. „ „ „ „ 4th day (posterior region of the trunk), × 200
Fig. 5*c*. „ „ „ „ 4th day (posterior region of the trunk), × 200
Fig. 5*d*. „ „ „ „ 4th day (posterior region of the trunk), × 200
Fig. 5*e*. „ „ „ „ 4th day (close to margin of rim), . × 200
Fig. 5*f*. „ „ „ „ 4th day (close to margin of rim), . × 200
Fig. 6. „ „ „ „ immediately posterior to fig. 5*b*, . × 500
Fig. 7. „ „ „ „ the two layers of fig. 5*e*, . . × 500
Fig. 8. „ „ „ „ the two layers of the blastodermic (extra-embryonic) area, . . . × 500
Fig. 9. *G. æglefinus*, 5th day, hind end of embryo, ... × 120
Fig. 10. „ 5th day, otocystic region, ... × 120
Fig. 11. *T. gurnardus*, 4th day, longitudinal section, ... × 135
Fig. 12. „ 4th day, slightly oblique longitudinal vertical section (nuchal region), . × 135
Fig. 13. „ oblique section through fore-brain and eye, ... × 135
Fig. 14. *P. flesus*, oblique longitudinal horizontal section of anterior end of embryo, . . × 200
Fig. 15. *G. æglefinus*, oblique longitudinal horizontal section of anterior end of embryo (rim at the equator of the egg), ... × 200
Fig. 15*a*. „ oblique longitudinal horizontal section on a lower plane than fig. 15, . × 200
Fig. 16. „ 4th day, oblique longitudinal horizontal section, further advanced than fig. 15, ... × 200
Fig. 17. *P. flesus*, transverse section at a later stage than fig. 4, ... × 120
Fig. 18. *Molva vulgaris*, horizontal section through the choroid fissure, ... × 400
Fig. 19. „ horizontal section through the choroid fissure at a lower plane than fig. 18, × 400
Fig. 20. „ transverse section through fore-brain, ... × 120

PLATE V.

Fig. 1. *Molva vulgaris*, front view of head, 6th day, ... × about 55
Fig. 2. *T. gurnardus*, pigment-spots on the trunk, 4th day, June 1886, ... × 250
Fig. 2*a*. „ yolk-sac, 1st day out, ... × 400
Fig. 2*b*. „ pigment-spot on yolk-sac (three stages in progress of corpuscle), . . × 400
Fig. 3. *P. limanda*, ovum with abnormal embryo, May 8, 1885, ... Enlarged
Fig. 3*a*. „ ovum with abnormal embryo, 3 days later, ... Enlarged
Fig. 4. Undermined ovum (F) with oil-globule (·034 inch in diam.), ... × 40
Fig. 5. *T. gurnardus*, cyclopean embryo *in ovo*, ... Enlarged
Fig. 6. *P. platessa*, ovum with embryo well-developed, April 20, 1886, ... × 40

Fig. 7. *Molva vulgaris*, aboral end of notochord, 10th day, ... ×200
Fig. 8. „ „ showing early pigment, 7th day, May 4, 1886, ... × 55
Fig. 9. „ „ embryo still further advanced, 8th day, May 5, 1886, . . . × 70
Fig. 10. „ „ ventral aspect of embryo, ... ×about 30
Fig. 11. *Pleuronectes limanda*, ovum showing protoplasmic reticulations, . . . ×about 40

PLATE VI.

Fig. 1. *G. morrhua*, surface view of ear, May 10, 1886, ... ×210
Fig. 2. *T. gurnardus*, surface view of ear, 7th day, June 22, 1886, ... ×205
The anterior edge is on the right, and the dorsal is superior.
Fig. 3. „ longitudinal vertical section of the otocystic region; 3 days old, June 1, 1886, ×230
Fig. 4. „ transverse section of the same region; 3 days old, June 1, 1886, . . ×230
Fig. 5. *G. æglefinus*, anterior end of larva, ... ×150
Fig. 6. Larva of *T. gurnardus*, from the dorsum, June 15, 1886, ... ×156
Fig. 7. *Pleuronectes platessa*, head of larva 2 days old, May 1886, ... Highly magnified
Fig. 8. *T. gurnardus*, sensory organ in integument behind the cephalic region, May 12, 1886, . ×156
Fig. 8*a*. „ sensory organ in integument behind the cephalic region, June 24, 1886, . ×415
Fig. 9. Transverse section through the otocystic region of larva of *G. æglefinus*, 19th day after hatching, ... ×about 300
Fig. 10. Section of the same region, ... ×230
Fig. 11. Otolith of *Cottus scorpius*, $\frac{1}{3\,5}$ in. long (·188 inch), showing strongly stained core and unstained concentric stratum, ... ×750

PLATE VII.

Fig. 1. *G. æglefinus*, transverse section, 13th day (7 hours before hatching), April 14, 1886, . ×200
Fig. 2. „ transverse section, 14th day after fertilisation (just emerged), . . ×150
Fig. 3. „ transverse section, 3rd day after hatching, April 24, 1886, . . . ×175
Fig. 4. „ transverse section, posterior to fig. 3, ... ×175
Fig. 5. „ transverse section through mid-gut and diverticulum (swim-bladder), . ×450
Fig. 6. „ transverse section, 2nd day out, April 24, 1886, ... ×200
Fig. 6*a*. „ transverse section (section succeeding fig. 6), ... ×200
Fig. 7. „ longitudinal horizontal section, 3rd day out, March 23, 1886, . . ×135
Fig. 8. *Molva vulgaris*, 6 days old, ventral aspect of the alimentary canal, . . . ×250
Fig. 9. *T. gurnardus*, longitudinal vertical section of the alimentary canal, 17th day, July 8, 1885, ×175
Fig. 10. „ dorsal view of pectoral fin of embryo before hatching, May 27, 1886, . ×210
Fig. 11. *G. morrhua*, section of the anal portion of the gut, 6th day out, May 4, 1886, . . ×175
Fig. 12. *Molva vulgaris*, longitudinal horizontal section through the hind-gut, 2 days old, May 7, 1886, ... ×175
Fig. 13. „ „ longitudinal horizontal section at a lower plane, ... ×175
Fig. 14. „ „ longitudinal horizontal section half-way down marginal fin, . . ×600
Fig. 15. „ „ longitudinal horizontal section of the anal opening, on a lower plane than fig. 14, ... ×600

PLATE VIII.

Fig. 1. Undetermined larva (D) with oil-globule (see p. 861), ... × 25
Fig. 2. *G. æglefinus*, 8th day after fertilisation, view of the heart, 8.50 P.M., March 30, 1886, . ×210
Fig. 3. *T. gurnardus*, from right side, focussed deeply: *pcw*, anterior pericardial wall, July 18, 1886, ... ×156
Fig. 4. „ ear, eye, and other organs, ... ×156
Fig. 5. „ 1st day, slightly oblique view of the cardiac region from below, June 1886, . ×156
Fig. 6. Head and anterior region of *T. gurnardus*, newly hatched, ... × 65
Fig. 7. Head of *G. æglefinus*, 7th day, April 30, 1886, ... × 65
Fig. 8. Branchial region of *T. gurnardus*, newly-hatched, ... × 90

Fig. 9. Heart and other organs of *T. gurnardus*, just hatched, seen from above, June 2, 1886, . × 90
Fig. 10. Young pleuronectid (unknown sp.), April 7, 1887, front face view, . . . × 50
Fig. 11. *T. gurnardus*, 4th day, transverse section through the heart, with mesoblast (*mes*), . × 600

PLATE IX.

Fig. 1. Anterior end of *T. gurnardus*, 3rd day, June 19, 1886, ... × 100
Fig. 2. *Molva vulgaris*, 4 days old, May 12, 1886, ... × 25
Fig. 3. „ „ 5 days old, May 13, 1886, ... × 25
Fig. 4. Head and anterior region of *P. platessa*, 8 mm. in length, and 4 days old, April 22, 1886, . × 40
Fig. 5. Anterior end of *T. gurnardus*, 8th day, June 24, 1886, ... × 55
Fig. 6. *G. æglefinus*, branchial and mandibular cartilages, April 20, 1886, . . . × 200
Fig. 7. Mandible of *G. æglefinus*, 10 days old, ... × 140
Fig. 8. Blastoderm of *T. gurnardus* at the stage of about sixty blastomeres: *x*, intra-blastomeric spaces apparently filled with fluid, ... × 40
Fig. 9. *Molva vulgaris*, margin of disc and nuclei of periblast, ... × 450
Fig. 10. *Gadus æglefinus*, 24th hour; the figure shows some marginal cells of the blastoderm, and a portion of the nucleated periblast, ... × 415

PLATE X.

Fig. 1. Slightly oblique view of the head of an advanced larva (15th day) of *Trigla gurnardus*, . × 40
Fig. 2. *Trigla gurnardus*, showing pigment in pectoral fin and visceral anatomy, 16th day, . Magnified
Fig. 2*a*. „ „ ventral view of same, 16th day, ... Magnified
Fig. 3. „ „ advanced embryo, 17th or 18th day, ... Magnified
Fig. 4. Blastodisc of *Trigla gurnardus* at the 6th hour, viewed from above; third furrow nearly completed. Oil-globule (*og*) seen below, ... × 80
Fig. 5. Larva of *Gadus morrhua*, ventral view of head, May 11, 1886, ... Magnified
Fig. 5*a*. „ „ „ dorsal view of head, May 11, 1886; the heart is indicated by the dotted lines, ... Magnified
Fig. 6. Opercular aperture of *Molva vulgaris*, May 10, 1886, ... × 205
Fig. 7. Zona radiata of an abnormal egg of *Solea vulgaris*, showing flat papillæ on the surface, . × 50
Fig. 8. Zona radiata of the pelagic egg with large perivitelline space with distinct punctures, . × 480
Fig. 9. Ovum of *Gadus morrhua* in the morula stage; blastomeres boldly spherical, . . × 50
Fig. 10. Ovum of *Pleuronectes flesus*, lateral view of the multicelled condition of the disc, . . × 35

PLATE XI.

Fig. 1. *G. æglefinus*, transverse section through the fore-brain, 17th day, ... × 200
Fig. 2. „ transverse section through the fore part of heart, ... × 200
Fig. 3. „ transverse section posterior to fig. 2, ... × 200
Fig. 4. „ transverse section through the fore part of the notochord, . . . × 200
Fig. 5. „ transverse section, lateral portion of section fig. 2, ... × 435
Fig. 6. *Molva vulgaris*, transverse section, branchial region and heart, 11th day, . . . × 135
Fig. 7. „ „ transverse section, branchial region and heart, 14th day, . . . × 135
Fig. 8. „ „ transverse section posterior to fig. 7, ... × 135
Fig. 9. *Gastrosteus spinachia*, longitudinal vertical section through the branchial region about the time of hatching, ... × 135
Fig. 10. „ „ longitudinal vertical section through the branchial region and operculum, slightly more advanced than fig. 9, . . . × 135
Fig. 11. *G. æglefinus*, 2 days old, oblique horizontal section of the branchial region, . . × 175
Fig. 12. *T. gurnardus*, section of a portion of the protoplasmic investment of the oil-globule, . × 450
Fig. 13. *Molva vulgaris*, section through the oil-globule, showing pigment in the protoplasm, . × 150
Fig. 14. *G. æglefinus*, 17 days old, transverse section through the hind-gut, . . . × 230
Fig. 15. „ transverse section through the base of the tail, ... × 230

Fig. 16. *G. æglefinus*, transverse section showing a tract, probably sensory, in the lateral region of the tail, ... × 230
Fig. 17. „ transverse section near the tip of the caudal trunk, ... × 230
Fig. 18. *T. gurnardus*, 22 days old, bony elements in the roof of the mouth, probably palatines, . × 120
Fig. 19. Clavicle of undetermined pleuronectid larva (possibly plaice), ... × 70
Fig. 20. *T. gurnardus*, 22 days old, premaxillary (?) elements: *a*, anterior extremity; *b*, posterior, . × 120

Plate XII.

Fig. 1. *T. gurnardus*, 1st day out, June 2, 1886, ... × about 32
Fig. 2. *G. morrhua*, advanced larva, May 2, 1855, ... × 45
Fig. 3. Early larva of *Motella mustela*, May 8, 1886, ... × 60
Fig. 4. *Molva vulgaris*, just hatched, 4.30 P.M., May 5, 1886, ... × 40
Fig. 5. *Cyclopterus lumpus*, newly-hatched, May 27, 1886, ... Magnified
Fig. 6. Larva of *Pleuronectes flesus*, 13 days old, April 26, 1886, ... × 50
Fig. 6*a*. „ „ „ 13 days old, dorsal view.
Fig. 7. Lateral view of the larva of *P. platessa*, May 7, 1886, ... × 40
Fig. 8. *G. æglefinus*, 6 days old, longitudinal vertical section through pericardial chamber, sinus venosus, and branchial arches, ... × 150

Plate XIII.

Fgi. 1. Larva of *Liparis montagui*, March 19, 1886, ... × 24
Fig. 2. Termination of the tail in the larva of *Cottus scorpius*, April 8, 1886, . . . × 40
Fig. 3. Ovum of undetermined pleuronectid (?), with large perivitelline space.
Fig. 4. *Molva vulgaris*, 1st day out, May 6, 1886, ... × 40
Fig. 5. *Centronotus gunnellus*, head and anterior region, March 18, 1886, ... × about 90
Fig. 6. „ „ early larva, March 14, 1886, ... Magnified
Fig. 6*a*. Caudal region of larval gunnel, ... × about 24
Fig. 7. *Centronotus gunnellus*, advanced larva, May 1, 1886, ... × about 24

Plate XIV.

Fig. 1. Embryo of *G. æglefinus*, removed from capsule, April 1, 1886, viewed somewhat obliquely, × 55
Fig. 2. Head of larva of *T. gurnardus*, 3rd day, ... × 55
Fig. 3. Abnormal tail of larva of *T. gurnardus*, 1st day, June 7, 1886, ... × 210
Fig. 4. Anterior end of larva of *Cottus scorpius* (?), April 8, 1886, ... × 24
Fig. 5. *P. platessa*, anal region, ... × 55
Fig. 6. Cardiac region of larva from ovum with large perivitelline space, ... × 40
Fig. 7. *T. gurnardus*, hind end of embryo and edge of blastopore, showing the adjoining nuclei of the periblast, ... × 210
Fig. 8. „ blastoderm shortly after the 6th hour, the 4th furrow in progress, . . × 80

Plate XV.

Fig. 1. *Molva vulgaris*, subnotochordal trunks and blood-elements *blc*, May 8, 1886, . . × 220
Fig. 2. Larva of *Liparis montagui* (?), showing vitelline circulation, April 12, 1886, . . × 40
Fig. 3. Aboral end of the notochord and tail of post-larval *P. flesus*, ... × 55
Fig. 4. Tip of the tail in the larval *Motella mustela*, ... × 220
Fig. 5. Marginal fin and part of alimentary canal in the larva of *Gastrosteus spinachia*, July 1, 1885 [the caudal fin in this figure has been marked *ef* instead of *cf*], . . . × 200
Fig. 6. *Cyclopterus lumpus*, lateral view, 26 days old, June 17, 1885, ... × 30
Fig. 7. Longitudinal section through the caudal portion of the notochord of *G. æglefinus*, 13th day, × 200
Fig. 8. *P. flesus*, head of young specimen, May 18, 1886, ... Magnified
Fig. 9. *Cyclopterus lumpus*, same age as in fig. 6, ventral view showing sucker-like ventral fins, . × 25

Plate XVI.

Fig. 1. *Pleuronectes flesus*, larva 13 days old, April 26, 1886, ... (reduced) × 40
Fig. 2. *Gadus merlangus*, early larva, April 24, 1885, ... × 40
Fig. 3. *Pleuronectes limanda*, 11 days old, May 22, 1886, ... × 56
Fig. 4. Dorsal view of the same, ... × 50
Fig. 5. Slightly oblique view of an advanced larva of *Pleuronectes platessa*, May 7, 1886, . . × 15
Fig. 5*a*. Slightly oblique view of an advanced larva of „ „ May 7, 1886, dorsal aspect, ... Magnified
Fig. 6. Anterior end of the larva of *P. limanda*, 8th day after emerging, May 19, 1886, . . Magnified
Fig. 7. Advanced larva of *Liparis montagui*, April 13, 1886, ... × 18
Fig. 8. Larva of *Trigla gurnardus*, 3rd day out, May 31, 1886, ... × 50
Fig. 9. Advanced larva of *Cottus scorpius*, April 13, 1886, ... × 18
Fig. 10. Abnormal ovum of *Trigla gurnardus*, July 8, 1885, ... × 40

Plate XVII.

Fig. 1. *Gadus æglefinus*, larva, 7 days old, with circulation active, April 19, 1886, . . . × 40
Fig. 2. *Motella mustela*, advanced larva, May 11, 1886, ... × 90
Fig. 3. *Cyclopterus lumpus*, artificially extruded from the egg-capsule, ... Enlarged
Fig. 4. Undetermined larva, with oil-globule, newly emerged from the ovum figured on Plate V. fig. 4, × 40
Fig. 5. *Trigla gurnardus*, post-larval stage, August 23, 1886, ... × 20
Fig. 6. „ „ post-larval stage, older stage, dorsal view, August 16, 1886, . . Enlarged
Fig. 7. „ „ post-larval stage, older stage, side view, August 16, 1886, . . Enlarged
Fig. 8. Young *Gadus morrhua*, June 11, 1886, ... About natural size
Fig. 9. Larva of *Molva vulgaris* on the 2nd day, May 8, 1886, ... × 50
Fig. 10. Larva of „ „ 13 days old, May 13, 1886, ... × 80
Fig. 11. Post-larval *Cottus quadricornis*, ... × 8
Fig. 12. Advanced larval stage of *Gadus merlangus*, ... × 50
Fig. 13. Newly-hatched larva of *Solea vulgaris*, ... × 52

Plate XVIII.

Fig. 1. Undetermined Pleuronectid, 24th hour after hatching, April 7, 1887, . . . × about 75
Fig. 2. Another undetermined Pleuronectid, 2nd day out (for ovum, *vide* Plate XIII. fig. 3), . × 40
Fig. 3. Post-larval ling (*Molva vulgaris*), showing long ventral fins, ... × 5
Fig. 4. Post-larval ling „ „ showing long ventral fins (later stage), . . . × 5
Fig. 5. Post-larval rockling (*Motella*), showing long ventral fins (later stage). The dorsal fin is entered in the text as *df*, ... × 6
Fig. 6. Post-larval rockling (*Motella*), younger stage than fig. 5, ... × 6
Fig. 7. Post-larval "witch" (*Pleuronectes cynoglossus*), ... × 4
Fig. 8. Post-larval "witch" „ „ older stage, ... × 5
Fig. 9. Advanced post-larval stage „ „ . . . . . × 5
Fig. 10. Advanced post-larval stage of armed bullhead (*Agonus cataphractus*), April 28, 1887, . × about 9
Fig. 11. Late larval stage of the same, April 4, 1887, ... × about 20

Plate XIX.

Fig. 1. Young turbot (*Rhombus maximus*), August 23, 1886, ... × about 10
Fig. 2. Post-larval stage of *Gadus morrhua*, in spirit, May 1887, ... × 6
Fig. 3. The same at a somewhat older stage than fig. 2, ... × 7
Fig. 4. Young *Cottus scorpius*, May 6, 1887, ... × 7
Fig. 5. Larval flounder (*Pleuronectes flesus*), 1st day out, ... × 50
Fig. 6. Post-larval stage of the angler (*Lophius piscatorius*), ... × 6
Fig. 7. Larval haddock (*Gadus æglefinus*), 1 day old, ventral aspect, ... × 35
Fig. 8. Larval cod (*Gadus morrhua*), 3rd day after hatching, . . Slightly larger than natural size

Fig. 9. Larval ling (*Molva vulgaris*), 5th day, May 2, 1886, ... × 90
Fig. 10. Larval example of undetermined Pleuronectid, obtained in St Andrews Bay 1887, . . × 90
Fig. 11. A young example of *Callionymus lyra*, 10 mm. in length, ... × 5
Fig. 12. Ovum of *Gadus morrhua* in the morula condition; blastomeres somewhat rounded, . × 60

PLATE XX.

Fig. 1. *Anarrhichas lupus*, larval tail showing radial striations, ... × 40
Fig. 2. „ „ larva just emerged, and viewed from the left side, January 28, 1886; the great vitelline vein is indicated through the semitransparent yolk, . × about 12
Fig. 3. Tail of the same at a more advanced stage, and when the blood-vessels form a fan, March 2, 1886, ... × 40
Fig. 4. Larva of *Anarrhichas lupus*, just emerged, viewed from the right side, January 28, 1886, . × about 12
Fig. 5. Dorsal view of a newly-hatched larva of the same species, January 1886, . . . × about 12
Fig. 6. Group of firmly adherent ova of the wolf-fish (*Anarrhichas lupus*), with embryos far advanced, ... Somewhat enlarged
Fig. 7. Fresh ovum (unimpregnated) of the same species, ... Somewhat enlarged
Fig. 8. Surface of lamina of the zona radiata in *Anarrhichas*, ... × 500
Fig. 9. Egg of salmon (*Salmo salar*): *a*, seen from above; *b*, viewed laterally, February 2, 1862, ... Somewhat enlarged
Fig. 10. Egg of the same species, similarly viewed and magnified.
Fig. 11. Portion of the zona radiata of the egg of the salmon, viewed as a transparent object, . × 300
Fig. 12. Caudal region of the embryo of *Gadus æglefinus*, 9th day after fertilisation, showing the neurenteric canal (?), ... × 70
Fig. 13. Rectal region in the larva of *Molva vulgaris*, showing the communication of the urinary vesicle with the early rectal lumen, ... × 70

PLATE XXI.

Fig. 1. Anterior end of larval *Anarrhichas lupus* seen from the right side, February 16, 1886, . × 24
Fig. 2. View of the circulation in the yolk-sac of the same species from the left side, February 23, 1886, ... × 44
Fig. 3. Yolk-sac of more advanced larva of *Anarrhichas*, with oil-globule on the right side, May 1, 1886, ... × 18
Fig. 3*a*. Yolk-sac of the same larva viewed from the left side, May 1, 1886, ... × 18
Fig. 4. Oblique view of the head of the larval *Anarrhichas*, January 1886, ... × 24
Fig. 5. Group of cells from the yolk-sac of the same form, ... × about 650
Fig. 5*a*. Altered blood-discs from larval *Anarrhichas*, ... × about 650
Fig. 6. Anterior end of segmental duct in the larval cod, May 10, 1886; reduced from a drawing × 200
Fig. 7. Sensory bodies beneath the epiblast on the under surface of the snout of embryo of haddock, 13th day after impregnation, ... × 435
Fig. 8. Horizontal section through the myotomes of the embryonic haddock on the 4th day after impregnation, ... × 435

PLATE XXII.

Fig. 1. *Solea vulgaris*, ovum in the lenticular stage, and showing a few of the vesicles of the yolk under the periblast. The cells of the blastoderm for simplicity have been omitted, . × 50
Fig. 2. Tail of late larval *Anarrhichas* in April, the margin being now crenate, and the vessels well developed, ... × about 60
Fig. 3. Vitelline circulation in the larval *Anarrhichas* on February 22, 1886, as seen from the right side, ... × 44
Fig. 4. Salmon, 1 day old, ... Slightly enlarged
Fig. 5. Abnormal yolk-sac of salmon, ... Slightly enlarged
Fig. 6. Salmon, 1 week old, ... Very slightly enlarged
Fig. 7. Yolk-sac of the salmon with the oleaginous sphere at the tip; an unusual position.

Fig. 8. Salmon about a fortnight old.
Fig. 9. Another example, slightly older, presenting differences in the outline of the yolk-sac and oil-globule.
Fig. 10. Salmon, 1 month old, viewed from the dorsum.
Fig. 11. Salmon, 5 weeks old, in profile.
Fig. 12. Embryo of the gurnard (*Trigla gurnardus*), showing early optic vesicles and myotomes, also compound vesicles anterior and posterior to Kupffer's vesicle, . . . × 50

Plate XXIII.

Fig. 1. Transverse vertical section (slightly oblique) of the head of the larval *Anarrhichas*, January 23, 1886, through the optic lobes, optic thalami, and anterior lobes: *ovf*, valve-like flap of the optic lobes, ... × 40
Fig. 2. Horizontal section through the anterior region of the same species, February 20, 1886, showing the fourth ventricle, parachordals abutting on the oral end of notochord, pronephros, and other parts, ... × 40
Fig. 3. Transverse vertical section through the fore-brain and the commencing optic lobes, the thalamencephalic chamber opening into the ventricle of the fore-brain beneath: *flm*, flap of mucous membrane at the side of the mouth, March 16, 1886, . . . × 40
Fig. 3*a*. Section somewhat behind the foregoing, showing the pineal gland and other parts, March 16, 1886, ... × 40
Fig. 4. Transverse vertical section through the infundibulum and lobi inferiores: *ms*, muscles; *ct*, connective tissue, June 20, 1886, ... × 97
Fig. 5. Transverse vertical section through the pineal region, showing the posterior commissural bands of fibres, June 20, 1886, ... × 97
Fig. 6. Transverse vertical (slightly oblique) section through the optic lobes and infundibulum of the same form, ... Magnified
Fig. 7. Transverse vertical section of tip of snout and through the nasal pits of the ling. The anterior epiblast is in contact with the hypoblast, ... × 135
Fig. 8. Caudal extremity and Kupffer's vesicle of the embryo of *Gadus æglefinus*, . . . × 45
Fig. 9. Embryo of *Gadus æglefinus*, showing neurenteric canal, 9th day after fertilisation, . . × 45
Fig. 10. Larva of *Solea vulgaris*, posterior aspect of the globular yolk, with large vesicles in proximity to the mass of oil-globules beneath the trunk, ... × 40

Plate XXIV.

Fig. 1. Longitudinal vertical section of the head of the larval *Anarrhichas* nearly in the median line, January 23, 1886, ... × 50
Fig. 2. Similar section on one side of the median line, ... × 40
Fig. 3. Transverse vertical section of the head of the same form through the tori semicirculares and commencement of the notochord, January 16, 1886, ... × 52
Fig. 4. Horizontal section through the anterior end of the fore-brain, with the olfactory bulbs (*olb*) and nerves (I.), June 20, 1886, ... × 52
Fig. 5. Transverse vertical section of the brain of *Anarrhichas*, just behind the anterior commissure, traces of which are still present in the section, January 16, 1886, . . . × 52
Fig. 6. Similar section behind the former, showing the roof of the fore-brain, and the inferior fibres, *fa*, behind the optic tract, January 16, 1886, ... × 52
Fig. 7. Circulation of the yolk-sac in the advanced larval *Anarrhichas* from the right side, March 31, 1886, ... Magnified

Plate XXV.

Fig. 1. Horizontal section through the heart and hyoid region of the larval *Anarrhichas*, March 29, 1886: *chy*, ceratohyal; *hhy*, hypohyal, ... × 60

Fig. 2. Horizontal section through the branchial arches of the same form, April 20, 1886. The branchial arches are indicated by the figures (Roman): *bbr*, basibranchial; *infp*, inferior pharyngeals; *bp*, branchial papillæ in section, ... × 52

Fig. 3. Transverse vertical section through the abdominal region of the advanced larval *Anarrhichas*, the hind-gut being severed just in front of the urinary vesicle, June 20, 1886, . × 55

Fig. 4. Similar section behind the foregoing, the termination of the hind-gut and the urinary vesicle being cut, May 1, 1886 : *ll*, remains of longitudinal ligament, . . . × 55

Fig. 5. Similar section through the urinary vesicle and anus (a more advanced stage), June 20, 1886, ... × 97

Fig. 6. Section posterior to the former through the urinary vesicle and its aperture in a post-larval form of the same date, ... × 97

Fig. 7. Section (transverse vertical) through the rectum and urinary vesicle in front of the previous sections, May 1, 1886, ... × 55

Plate XXVI.

Fig. 1. Intestine of the larval *Anarrhichas*, showing the circulation from the left side, February 1886, ... × 40

Fig. 2. Similar view from the same form, seen from the right side, February 20, 1886, . . × 24

Fig. 3. Transverse vertical section through the kidney of the same form at an advanced stage, June 20, 1886, ... × 230

Fig. 4. Transverse vertical section through the glomerulus in the same species, March 1, 1886, ... Highly magnified

Fig. 5. Transverse section of the notochord of a salmon of the first day, showing nuclei and notochordal investments, ... Highly magnified

Plate XXVII.

Fig. 1. Young *Anarrhichas lupus* reared in the St Andrews laboratory, May 14, 1886, . × about 12

Fig. 2. Circulation in the tail of the larval *Anarrhichas*, March 13, 1886, ... × 25

Fig. 3. Caudal region of the advanced larval *Anarrhichas*, showing the constrictions of the notochord opposite the attachment of the neural and hæmal arches, May 4, 1886, . . × 24

Fig. 4. Transverse section of the alimentary canal (stomachal region) of the advanced larval *Anarrhichas*, June 20, 1886, ... × 150

Fig. 5. Transverse section of the œsophageal region of the alimentary canal, with the anterior end of the heart below, March 29, 1886, ... × 150

Fig. 6. Transverse section of the same region of the canal, January 16, 1886, . . . × about 60

Plate XXVIII.

Fig. 1. Aboral termination of notochord and caudal circulation in the larval salmon (*Salmo salar*), 1 day old, ... Magnified

Fig. 2. Lateral view of the circulation in the region over the ventral fin in a larval salmon of the same age, ... Magnified

Fig. 3. Capillaries in the region of the fatty fin (of the larva of the same species) in course of development, ... Magnified

Fig. 4. Ovum of the haddock (*Gadus æglefinus*), 5th hour; the two blastomeres are of unequal size, ... × 60

Fig. 5. Ovum of the ling (*Molva vulgaris*), 4th day after fertilisation; blastopore much reduced; embryonic thickening very marked, ... × 50*

* This figure was drawn by Mr Prince.

CONTENTS.

PAGE

I. General Remarks, ... 665

II. The Mature Ovum, ... 666
General Features, ... 666
Pelagic Ova, ... 669
Distribution, ... 670
Dimensions of Ova, ... 670
The Egg-Capsule, with Remarks on the Reproductive Organs and Period of Spawning, ... 671
Liparis montagui, ... 673
Cyclopterus lumpus, ... 674
Agonus cataphractus, ... 674
Cottus scorpius, ... 675
Ammodytes tobianus, ... 675
Gobius ruthensparri, ... 676
Centronotus gunnellus, ... 676
Blennius pholis, ... 677
Blenniops ascanii, ... 677
Motella mustela, ... 677
Other species, ... 679
The Micropyle, ... 682
Deutoplasm, or Food-Yolk, ... 684
Oleaginous and other Globules, . . 687
Perivitelline Space, ... 688

III. Extrusion and Deposition, . . . 688
Fertilisation, ... 690
Polar Globules, ... 693
Movements of the Yolk, ... 696

IV. Segmentation, ... 698
The Cortical Protoplasm, ... 698
Subgerminal Disc, ... 701

V. The Blastoderm, ... 703
The Germinal Cavity, ... 709

VI. The Periblast, ... 714

VII. The Embryonic Shield, ... 721
Epiblast, ... 726
Mesoblast, ... 727
Hypoblast, ... 730
The Blastopore, ... 731
Kupffer's Vesicle, ... 732
Neurenteric Canal, ... 734
Medullary Groove and Primitive Streak, ... 736

VIII. General Development of the Trunk, 739
Epiblast—Epidermal Stratum, . . 739
„ Neurodermal Stratum, . 739
Notochord, ... 740

PAGE

VIII. General Development of the Trunk—*continued.*
Vertebral Column, ... 745
Branchial System, ... 747
Skull, ... 752
Brain, ... 755
Auditory Organs, ... 760
Olfactory Organs, ... 762
Optic Nerves and Vesicles, . . . 763
Cranial Nerves, ... 768
Lateral Sense-Organs, ... 769
Alimentary Canal, ... 770
„ „ , Mouth, . . . 773
„ „ , Anus, . . . 774
Liver, ... 774
Swim-Bladder, ... 774
Heart and Circulation, ... 775
Renal Organs, ... 783
Integument and Embryonic Pigmentation, ... 788
Ova and Generative Organs, . . 793

IX. The Fins—(*a*) Median Unpaired Fins, . 795
„ „ (*b*) Caudal Fin, . . . 799
„ „ (*c*) The Paired Fins, . . 800

X. Methods and Technique, . . . 803

XI. The Embryonic, Larval, and Post-Larval Stages, ... 806
Trigla gurnardus, ... 806
Gadus morrhua, ... 812
Gadus æglefinus, ... 822
„ *virens*, ... 823
„ *merlangus*, ... 824
Molva vulgaris, ... 827
Motella mustela, ... 832
Unknown Egg and Larva (F), (Motella-like in size), ... 835
Unknown Larva (E), ... 835

Young Pleuronectidæ, ... 835
Hippoglossoides limandoides, . . . 835
Pleuronectes limanda, ... 837
„ *cynoglossus*, ... 839
„ *platessa*, ... 840
„ *flesus*, ... 841
Rhombus maximus, ... 845
„ *laevis*, ... 847
Solea vulgaris, ... 848
Zeugopterus punctatus, ... 852
Unknown Larval Pleuronectid (A), with oil-globule, ... 852

PAGE

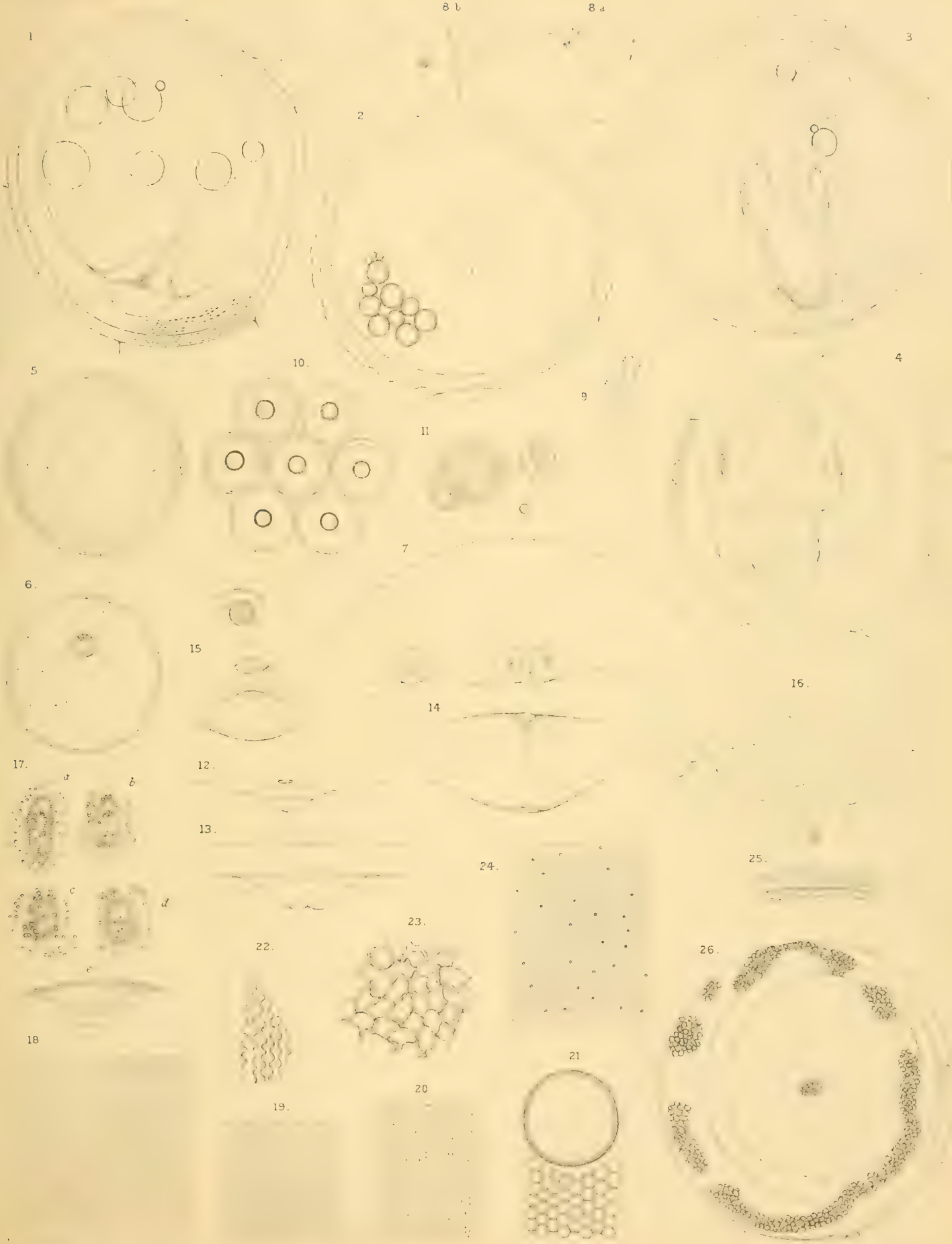
Young Pleuronectid—*continued.*
Ovum of Pleuronectid (B) with large perivitelline space, ... 853
Unknown Pleuronectid Larva (C), . 853
Clupea harengus, ... 854
„ *sprattus*, ... 857
Ammodytes tobianus, ... 858
Unknown Species (D), ... 860
„ „ (G), ... 861
Cottus, ... 861
Agonus cataphractus, ... 862
Callionymus lyra, ... 864
Liparis montagui, ... 866
Centronotus gunnellus, ... 867
Lophius piscatorius, ... 869

XII. General Remarks on the Post-Larval Fishes, ... 870
Monstrosities, ... 874

XIII. *Anarrhichas lupus*, Development and Life-History compared with *Salmo salar* and certain other forms, ... 874
Vitelline Circulation, ... 876
Circulation in the Trunk, ... 880
„ „ Tail, ... 884

PAGE

XIII. *Anarrhichas lupus*, Development and Life-History compared with *Salmo salar* and certain other forms—*continued.*
Pigment, ... 886
Integument, ... 889
Serous Spaces, ... 889
Pectoral Fins, ... 890
Median Unpaired Fins, ... 891
Caudal Trunk, ... 893
Notochord, ... 896
Skull, ... 898
Hyoid Arch, ... 904
Vertebral Column, ... 905
Ribs, ... 907
Brain, ... 908
Spinal Cord and Lateral Line, . . 916
Ear, ... 916
Olfactory Organ, ... 918
Sensory Organs in the Snout, . . 918
Alimentary System, ... 919
Swim-Bladder of certain forms, . . 922
Liver, ... 923
Spleen of certain forms, ... 924
Branchial System, ... 924
Renal Organs, ... 925
Body-Cavity, ... 928



W. C. M. del., R. Scharff, Fig. 25, E. E. Prince Fig^s 5-9, 17 & 23.

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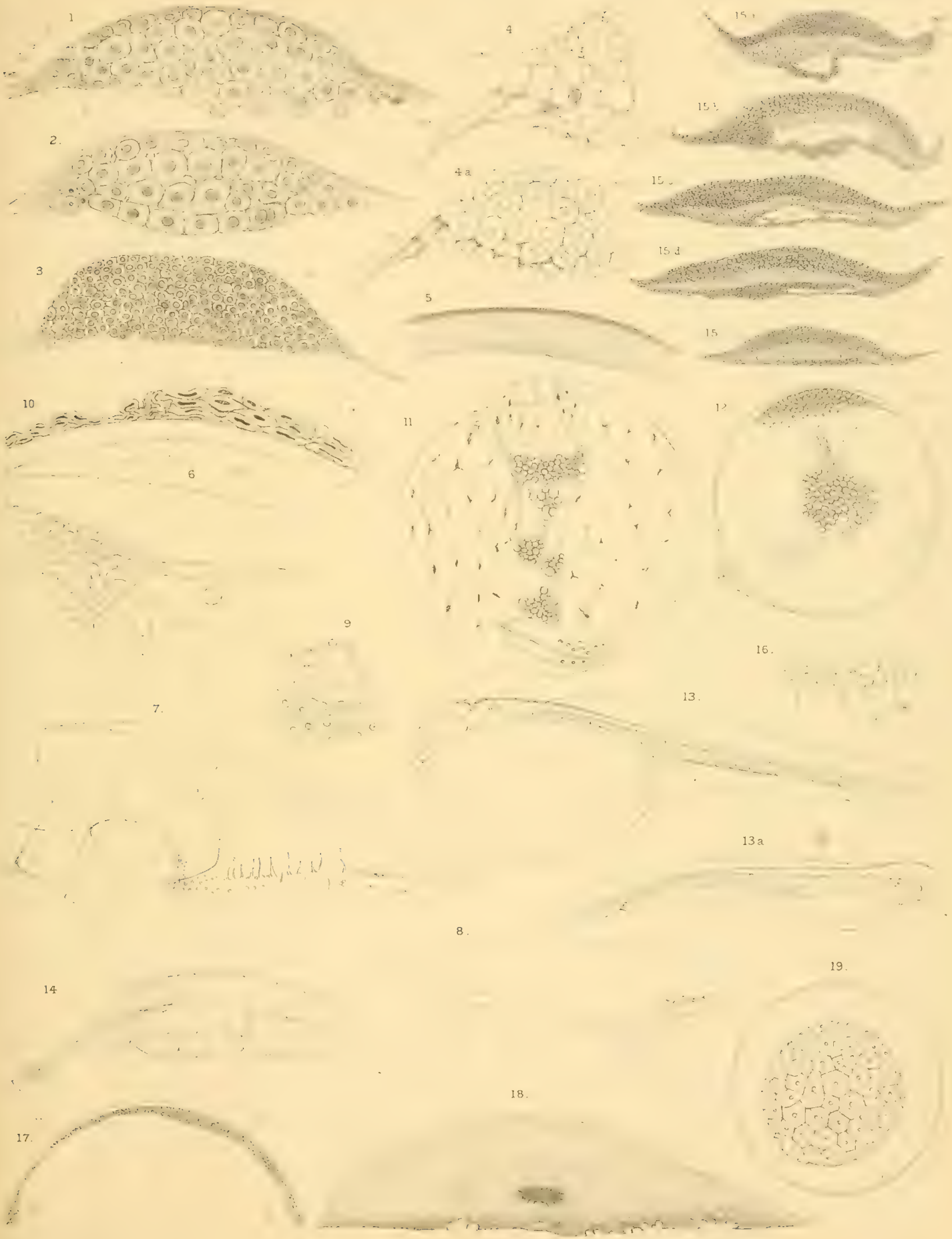
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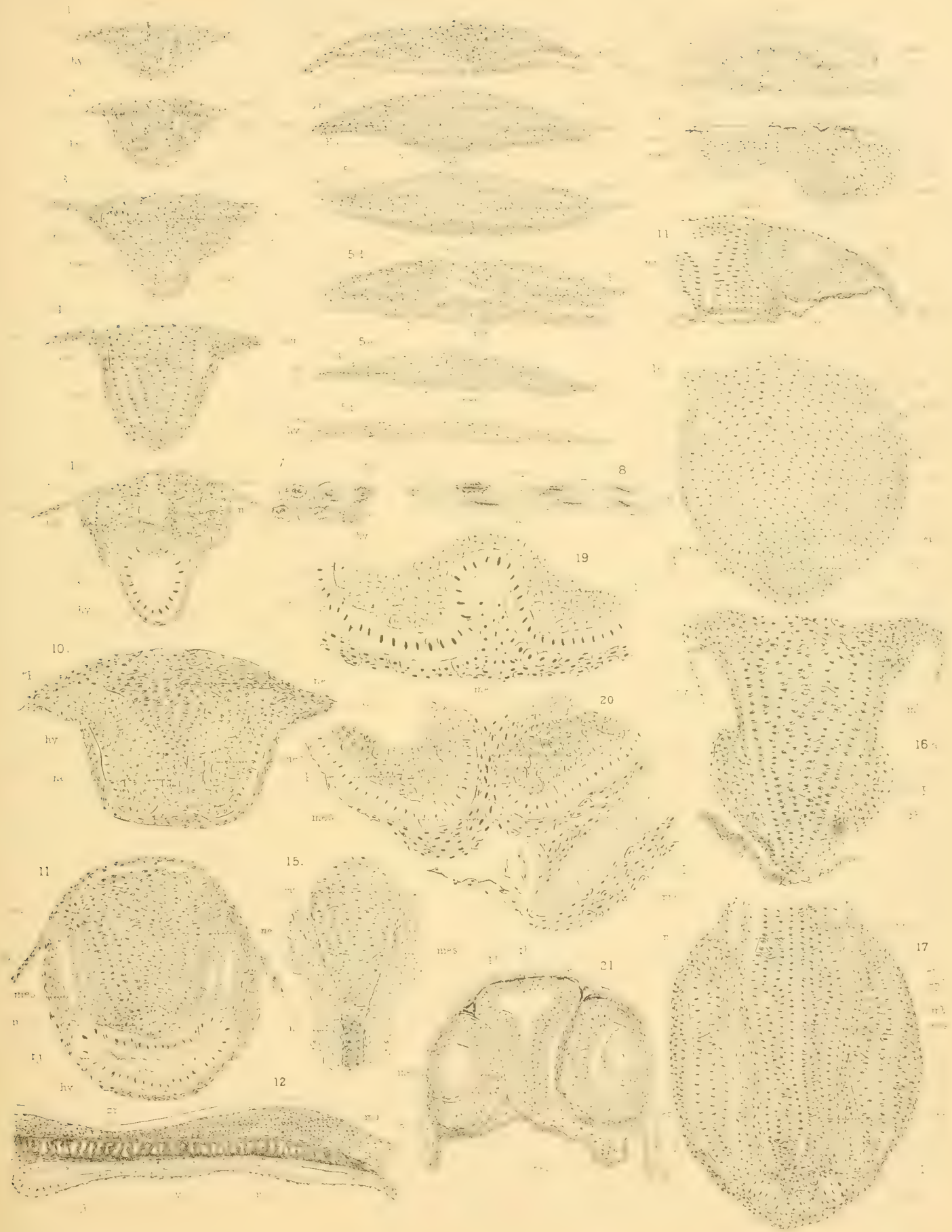

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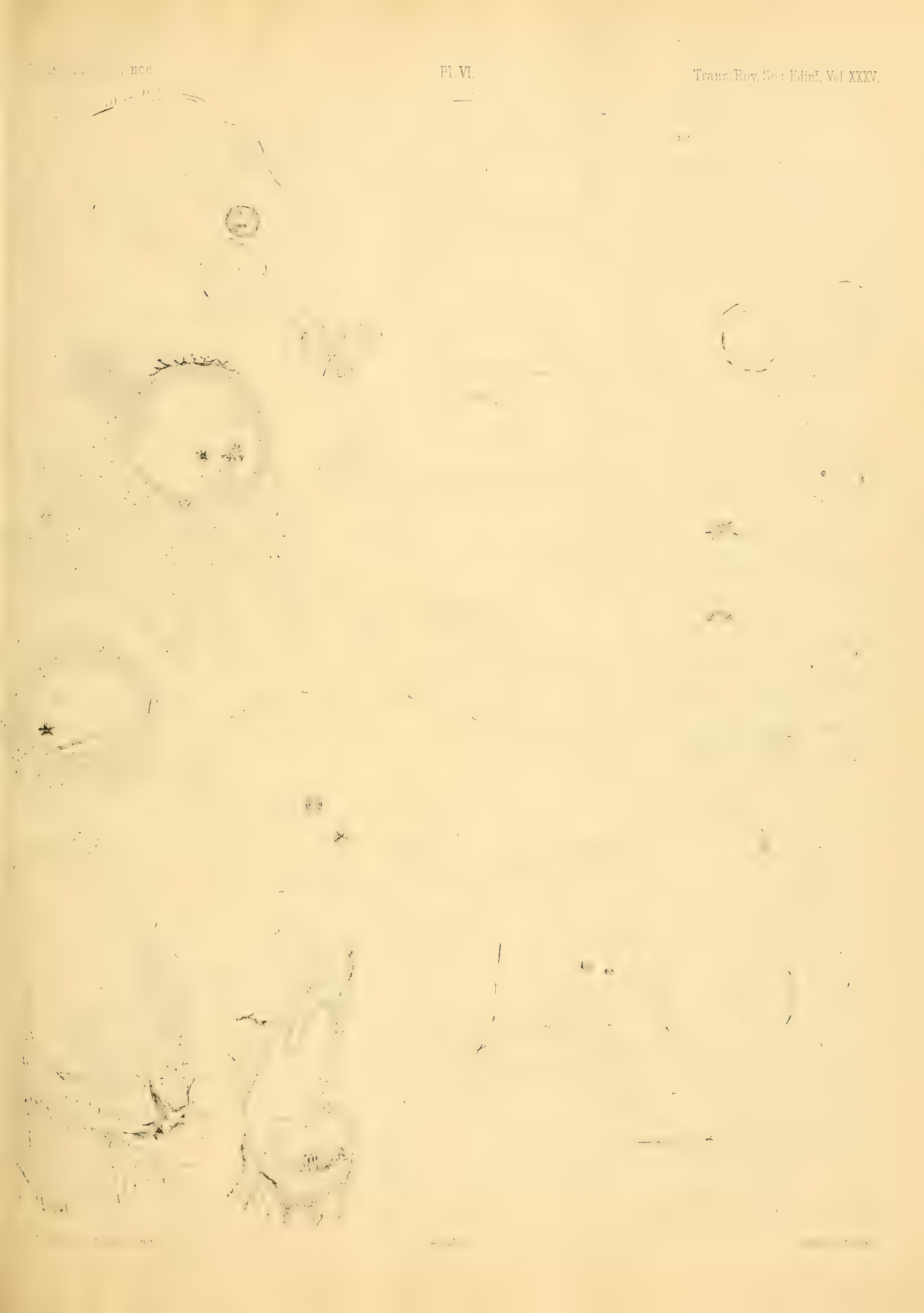

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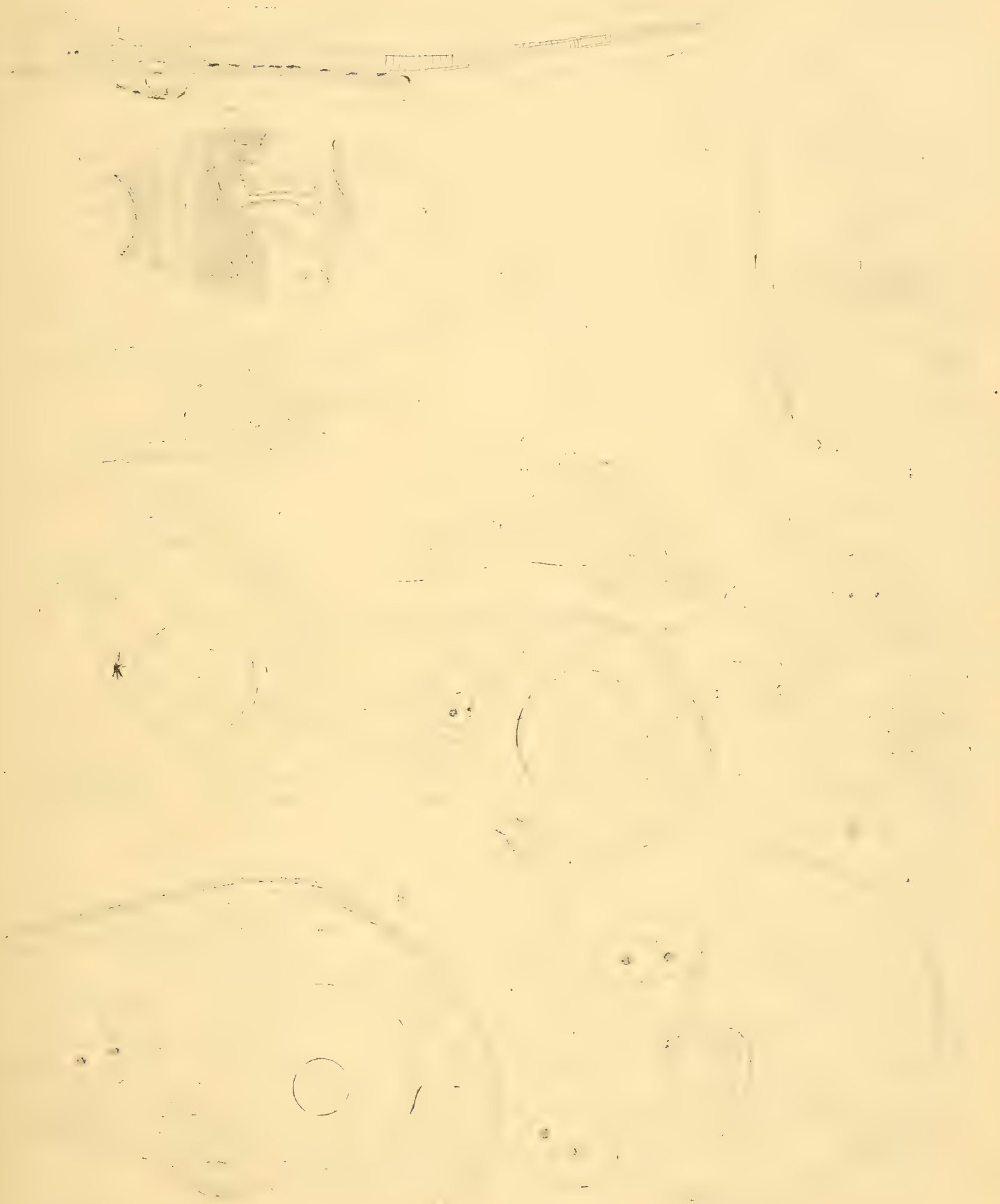

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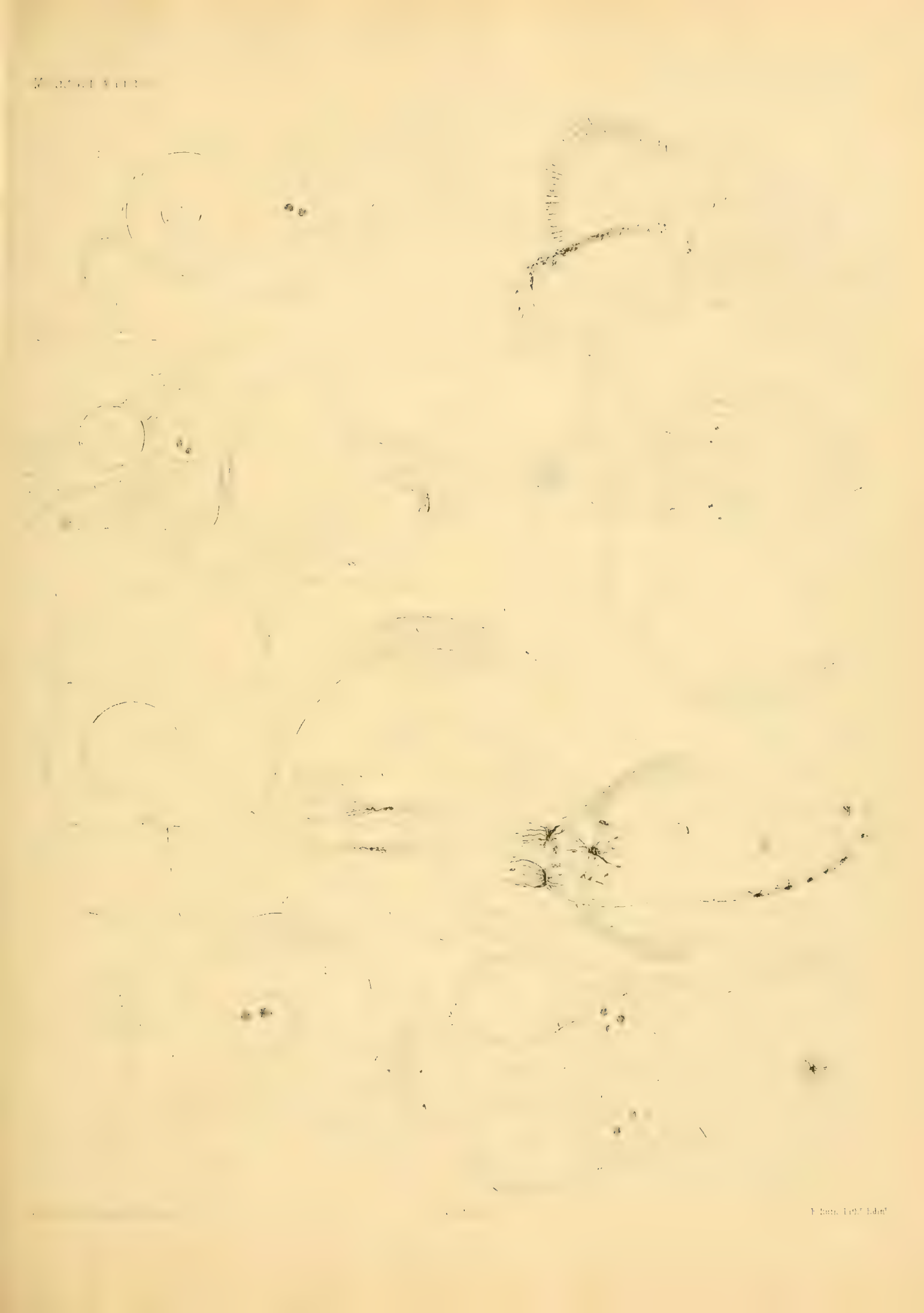

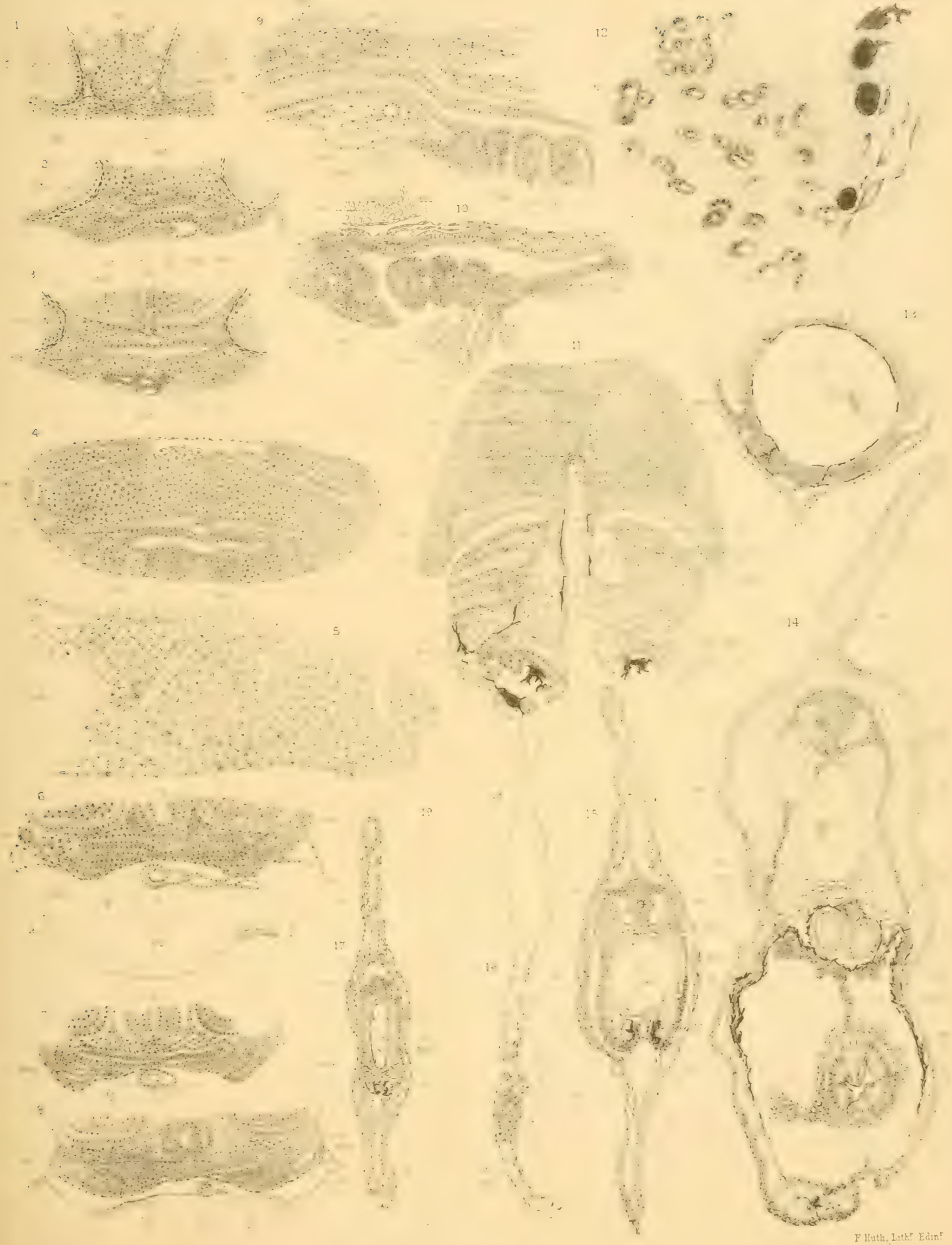
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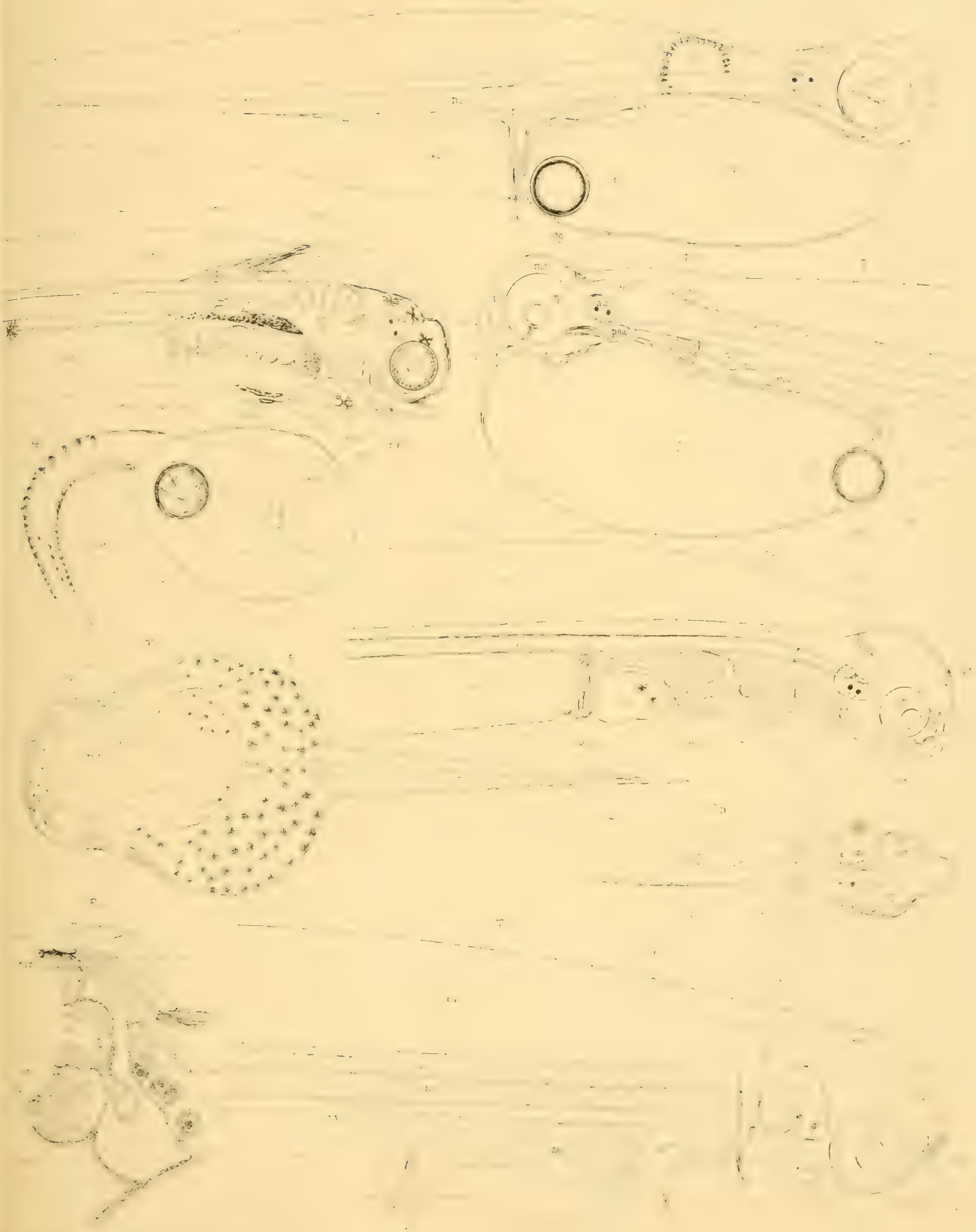
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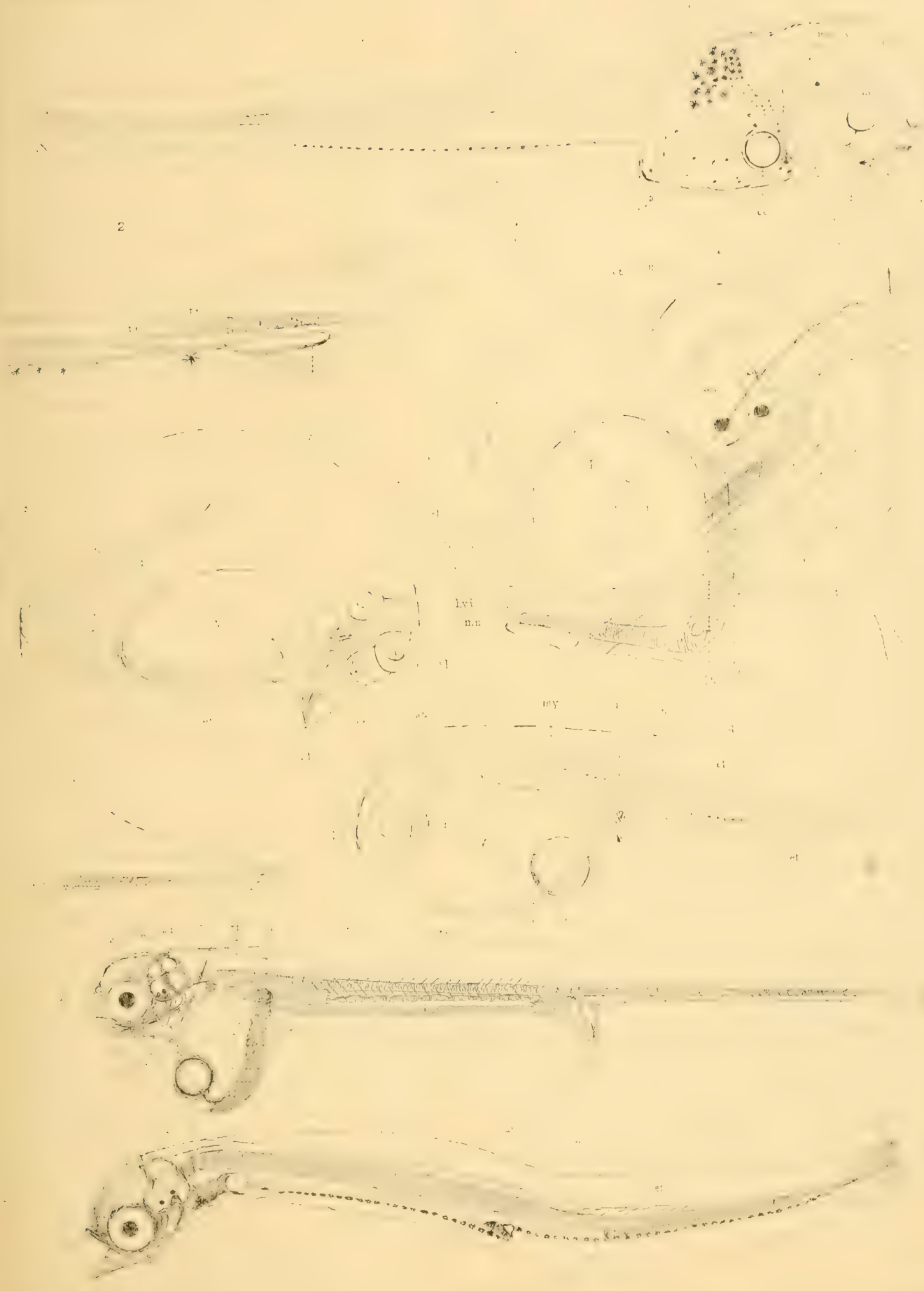
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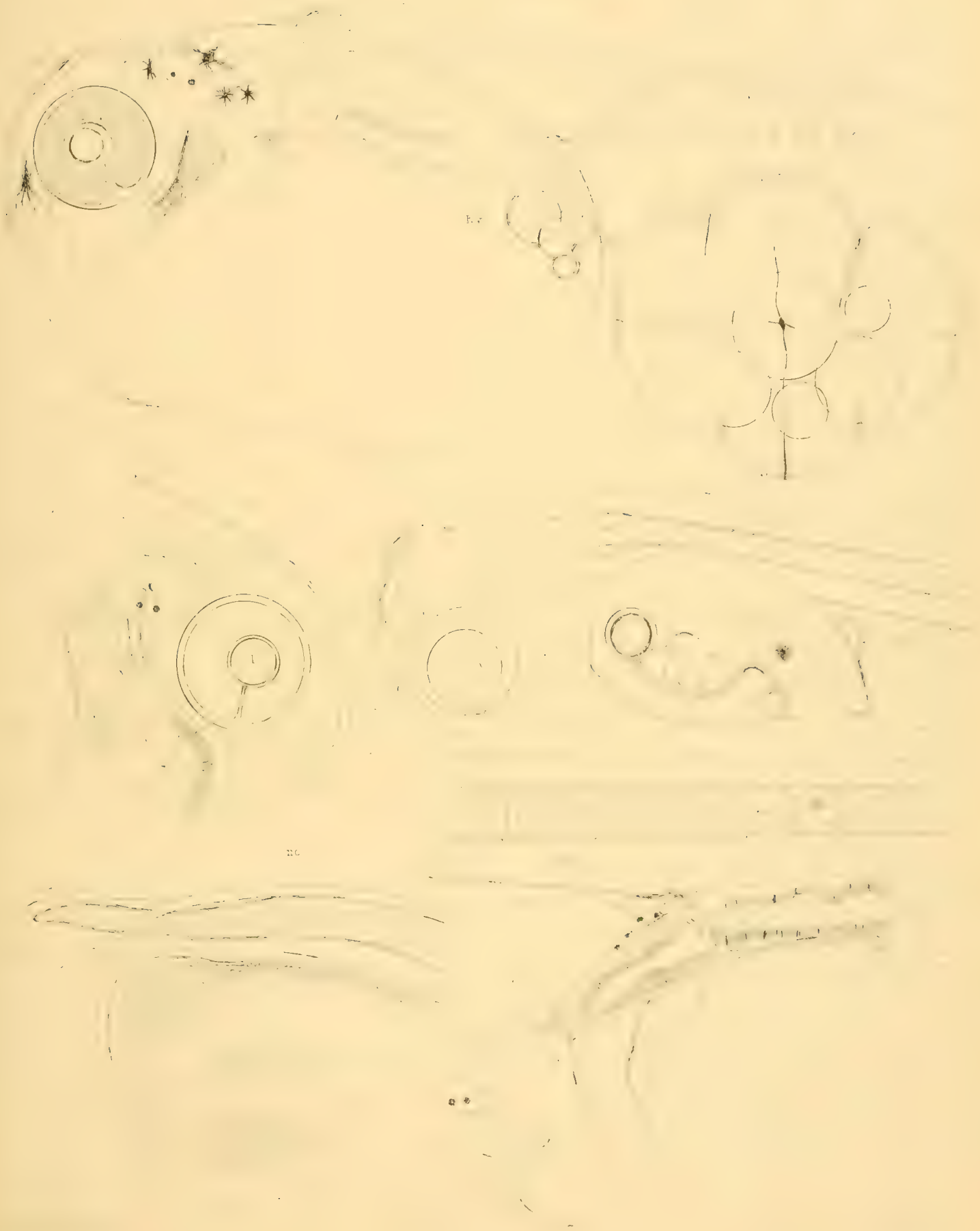

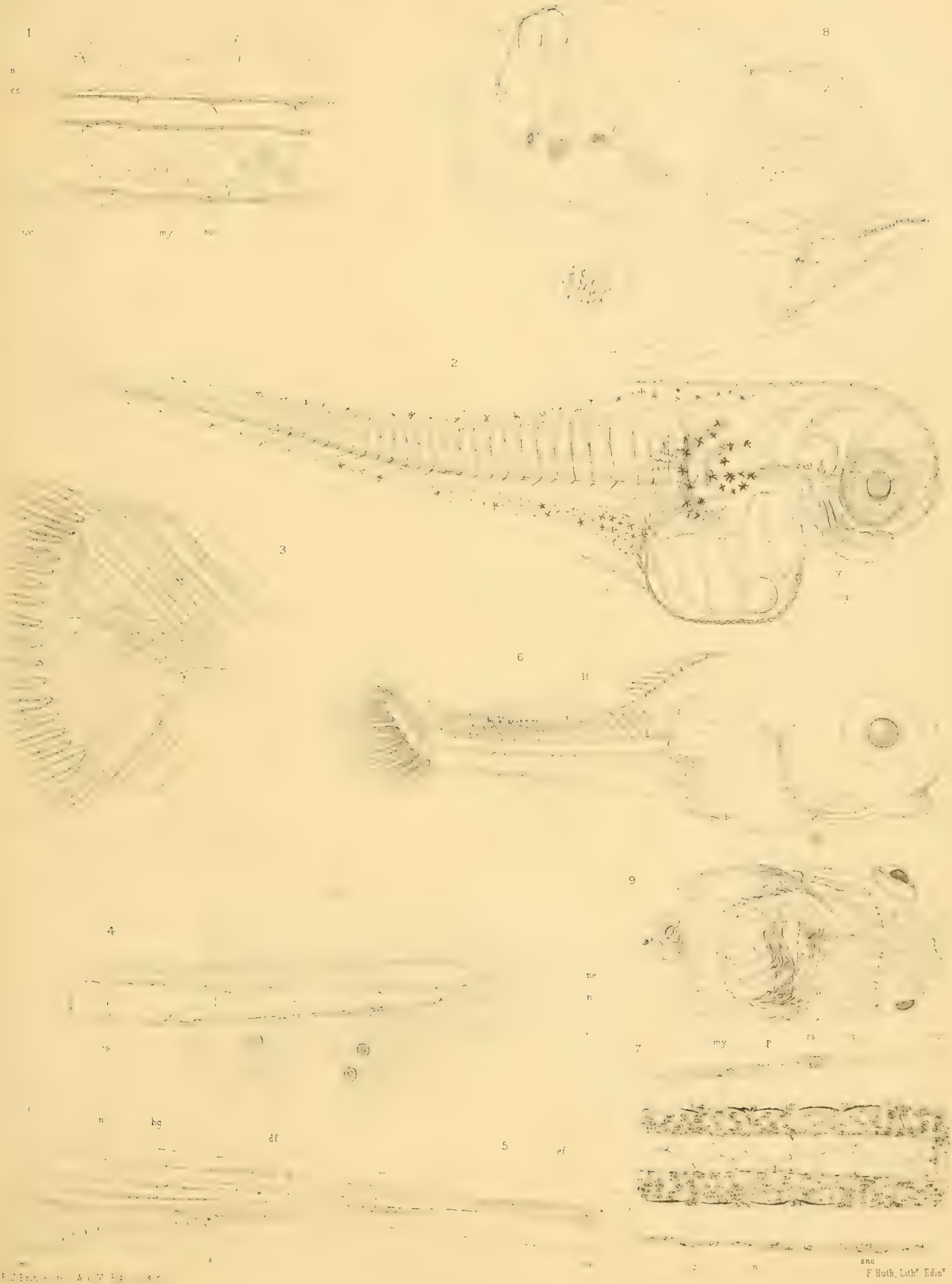

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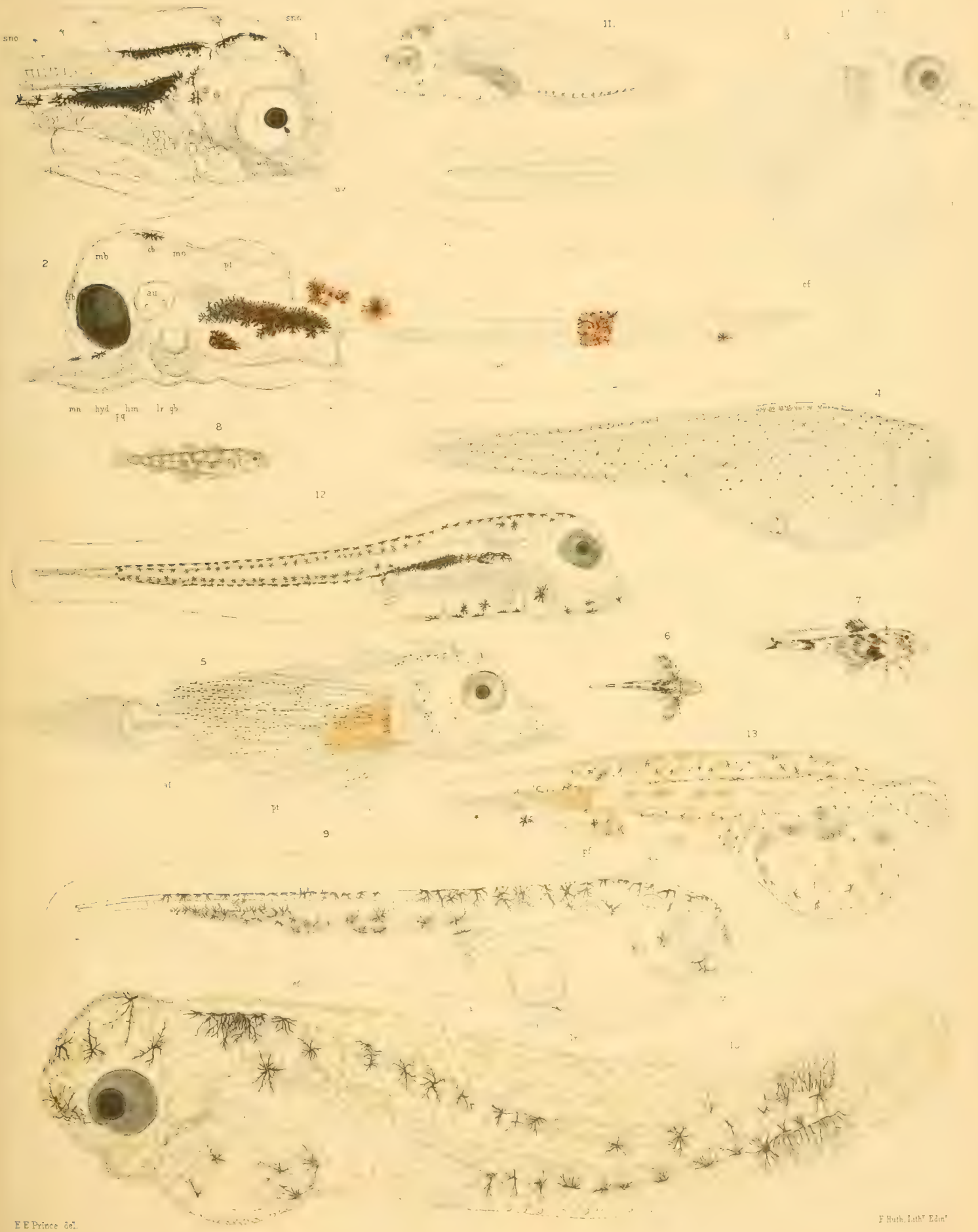

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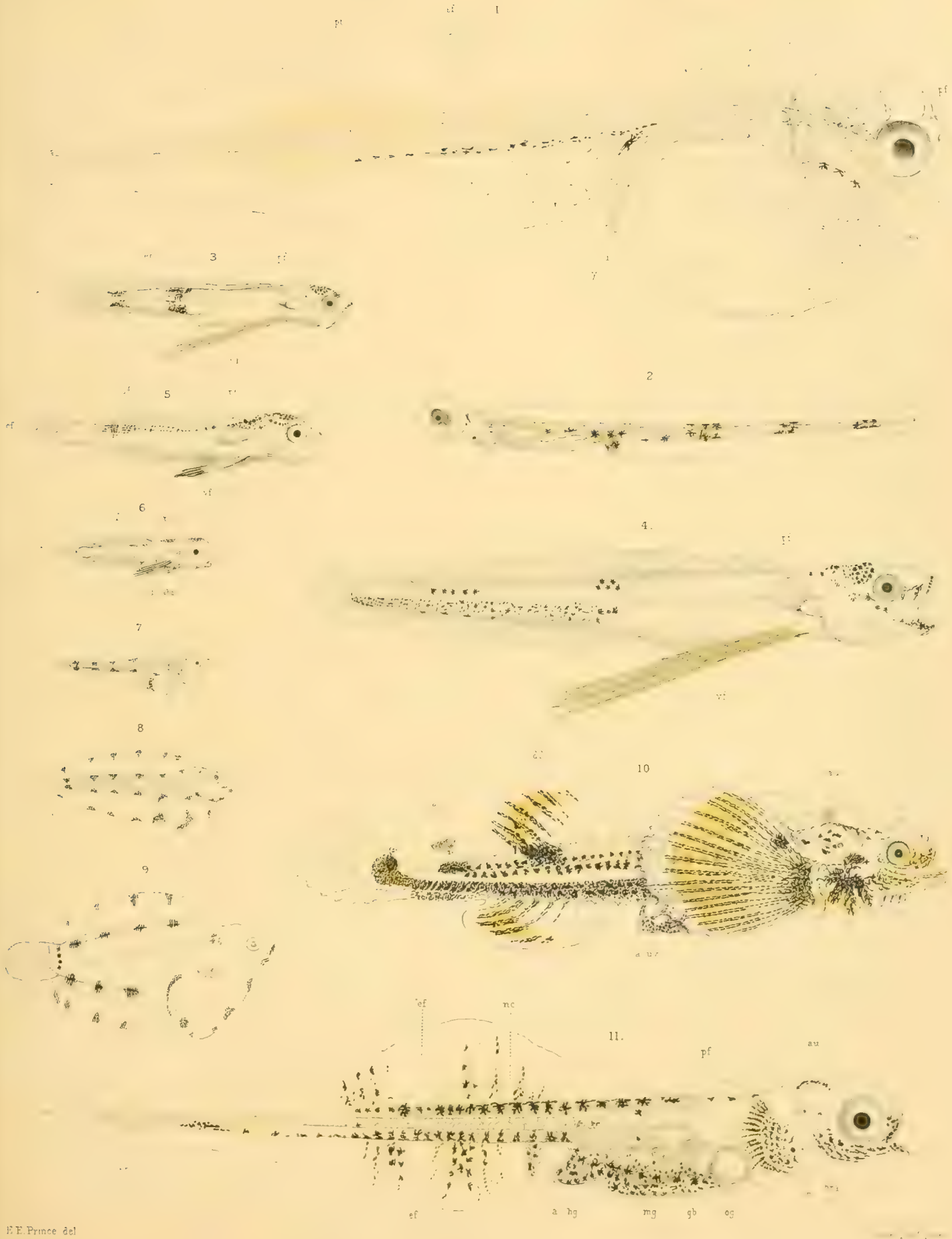

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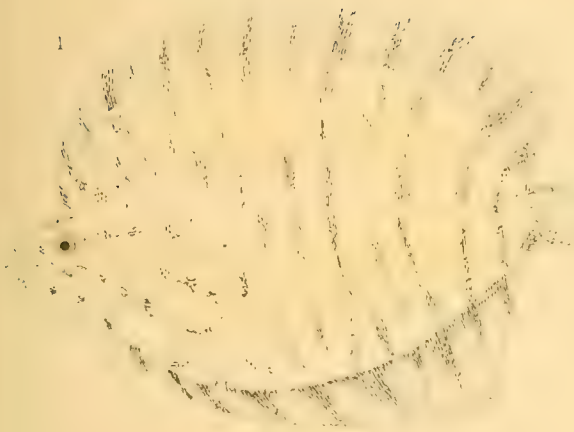

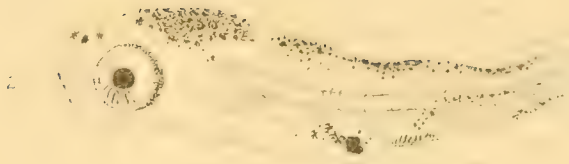

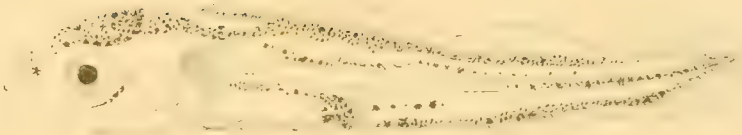

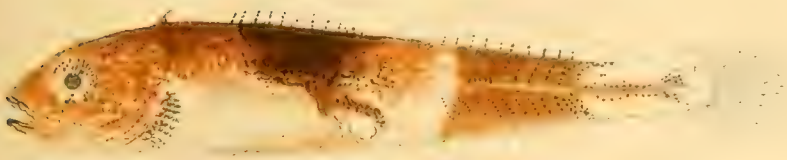

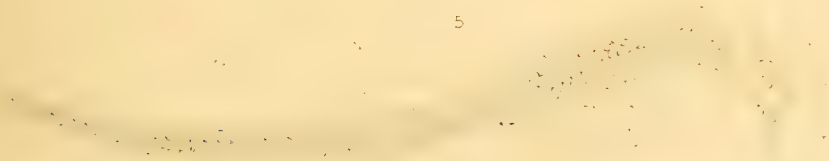

F.E. Prince del., R. Scharff, Fig. 11

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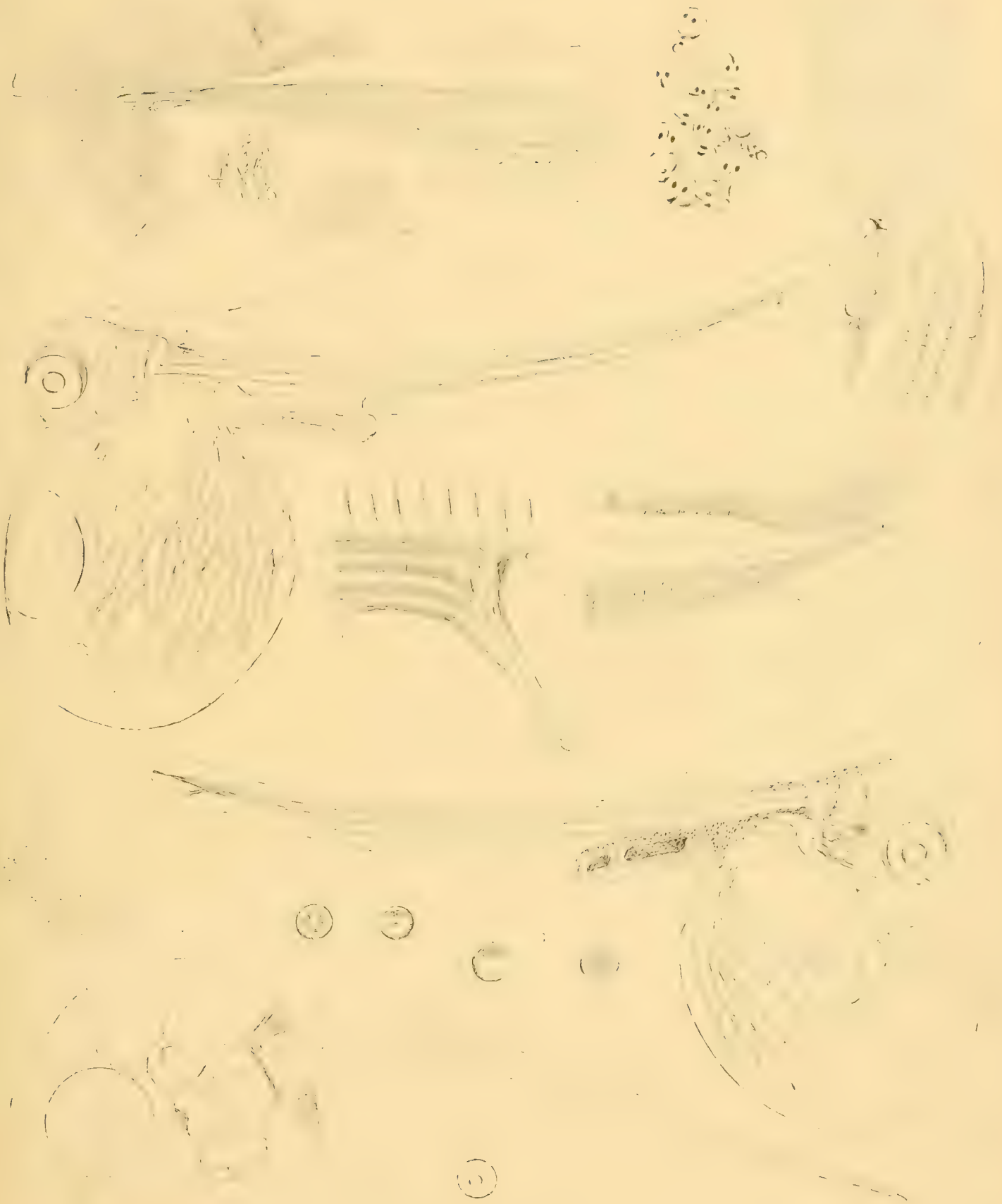

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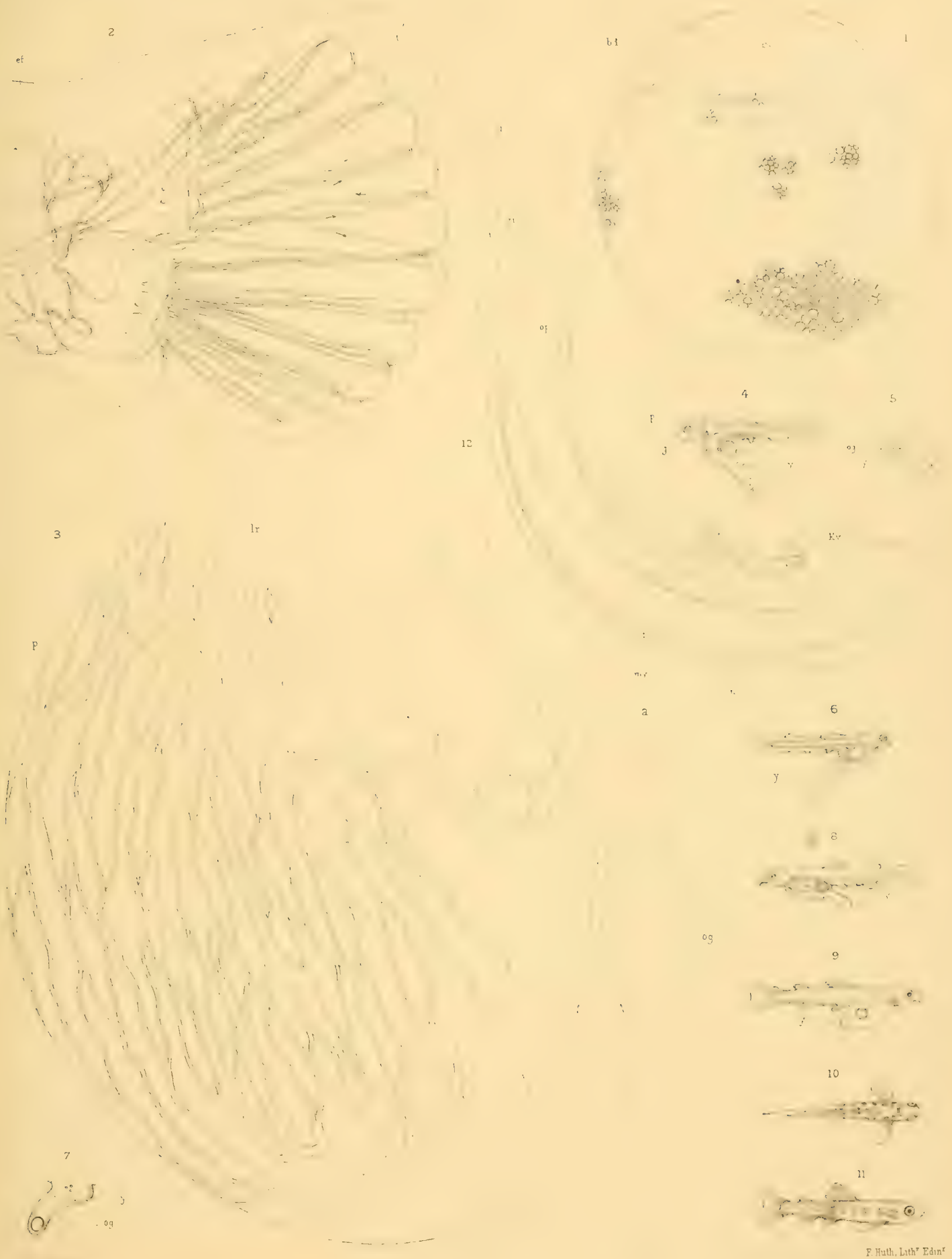

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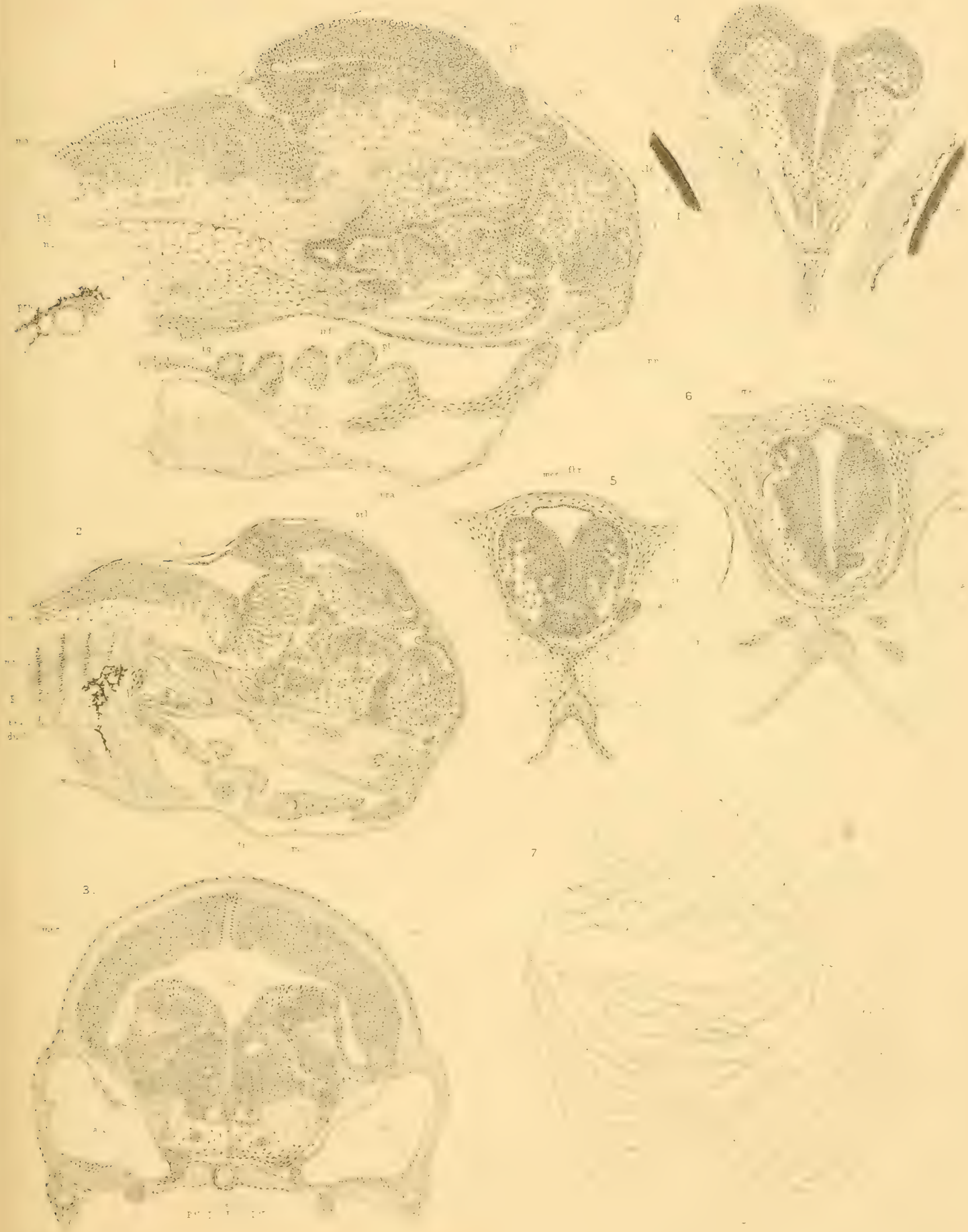

Prince del, Fig 7 W C M.

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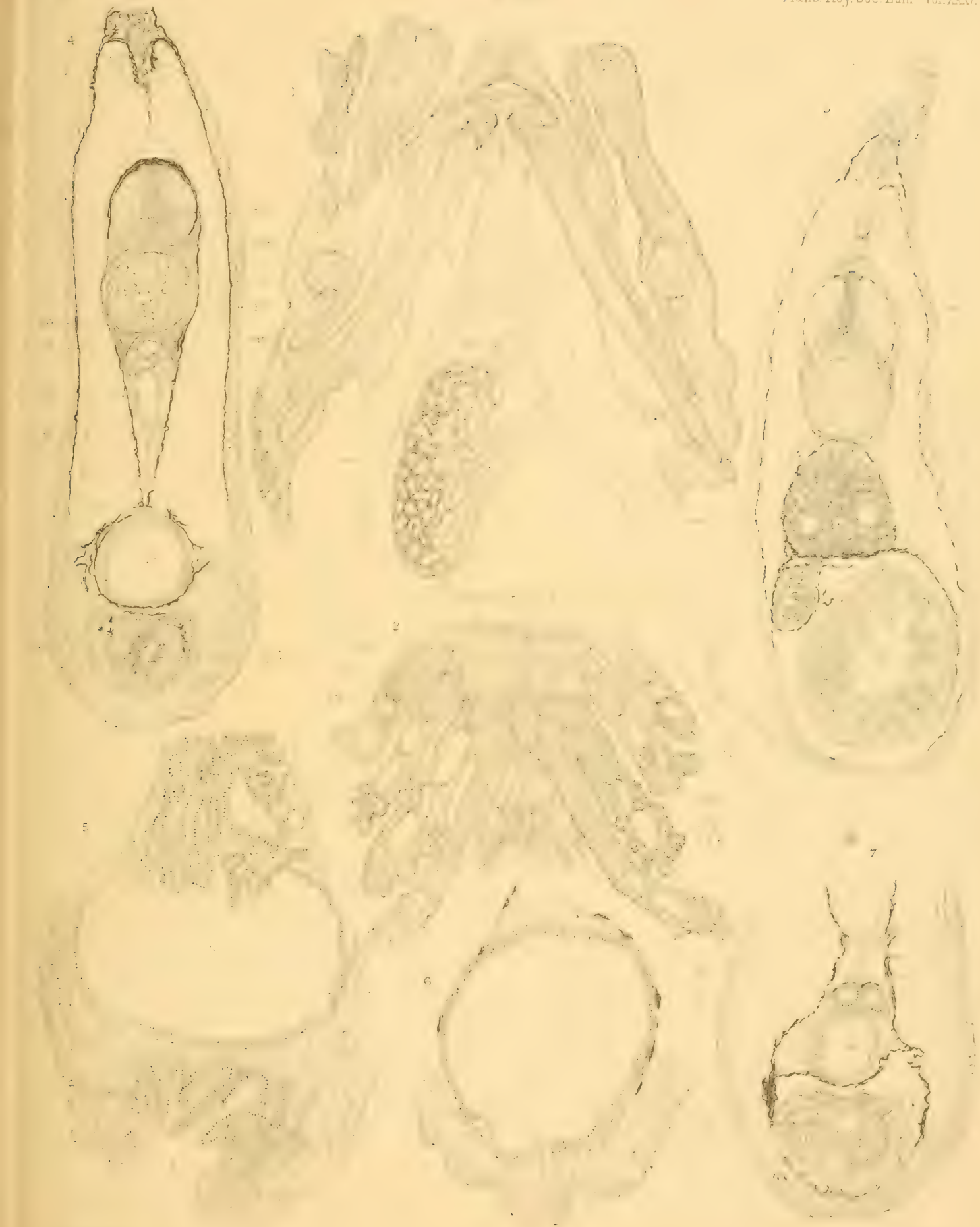
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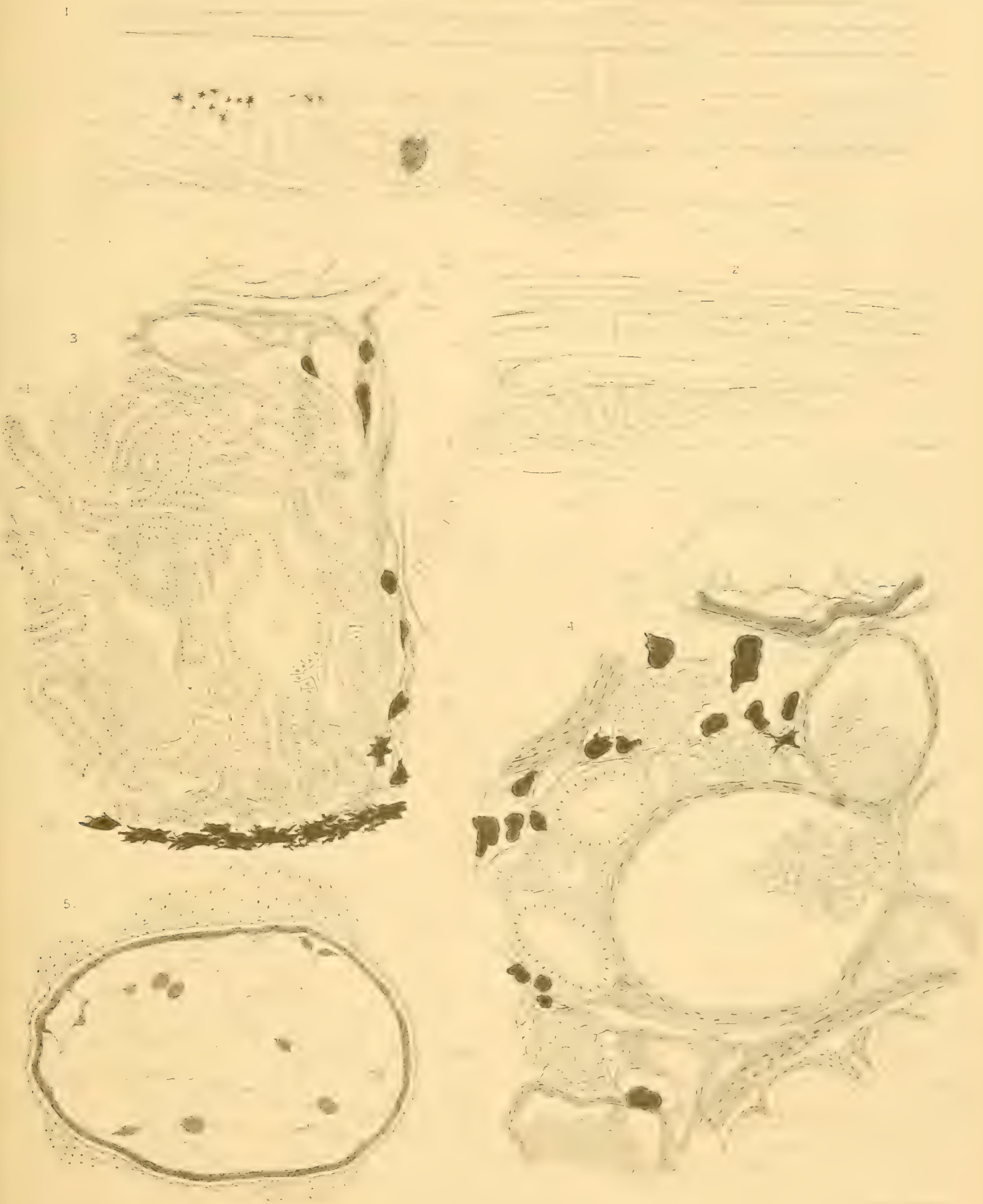

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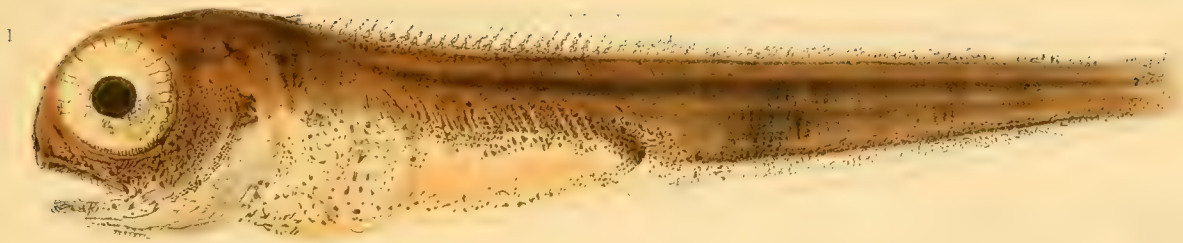

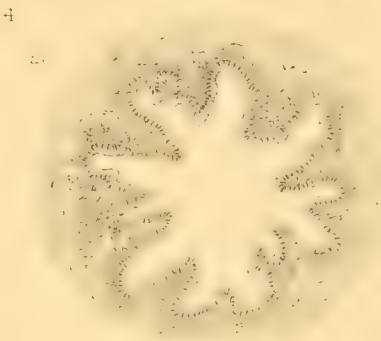

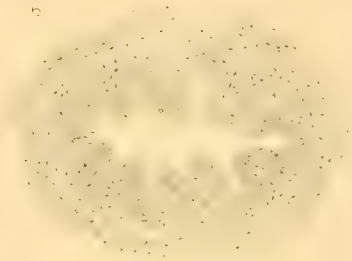

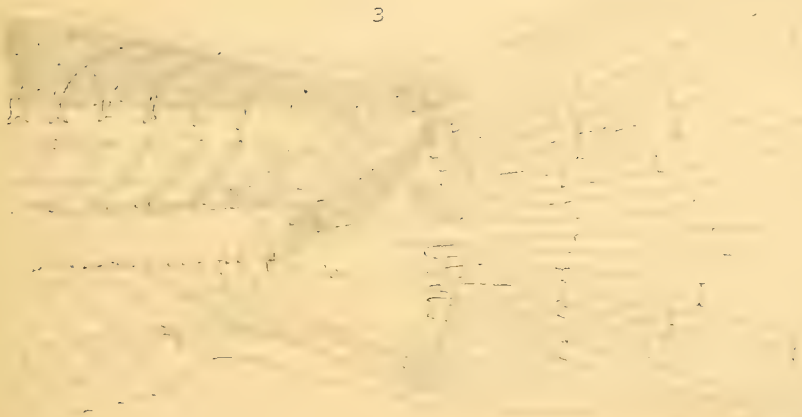

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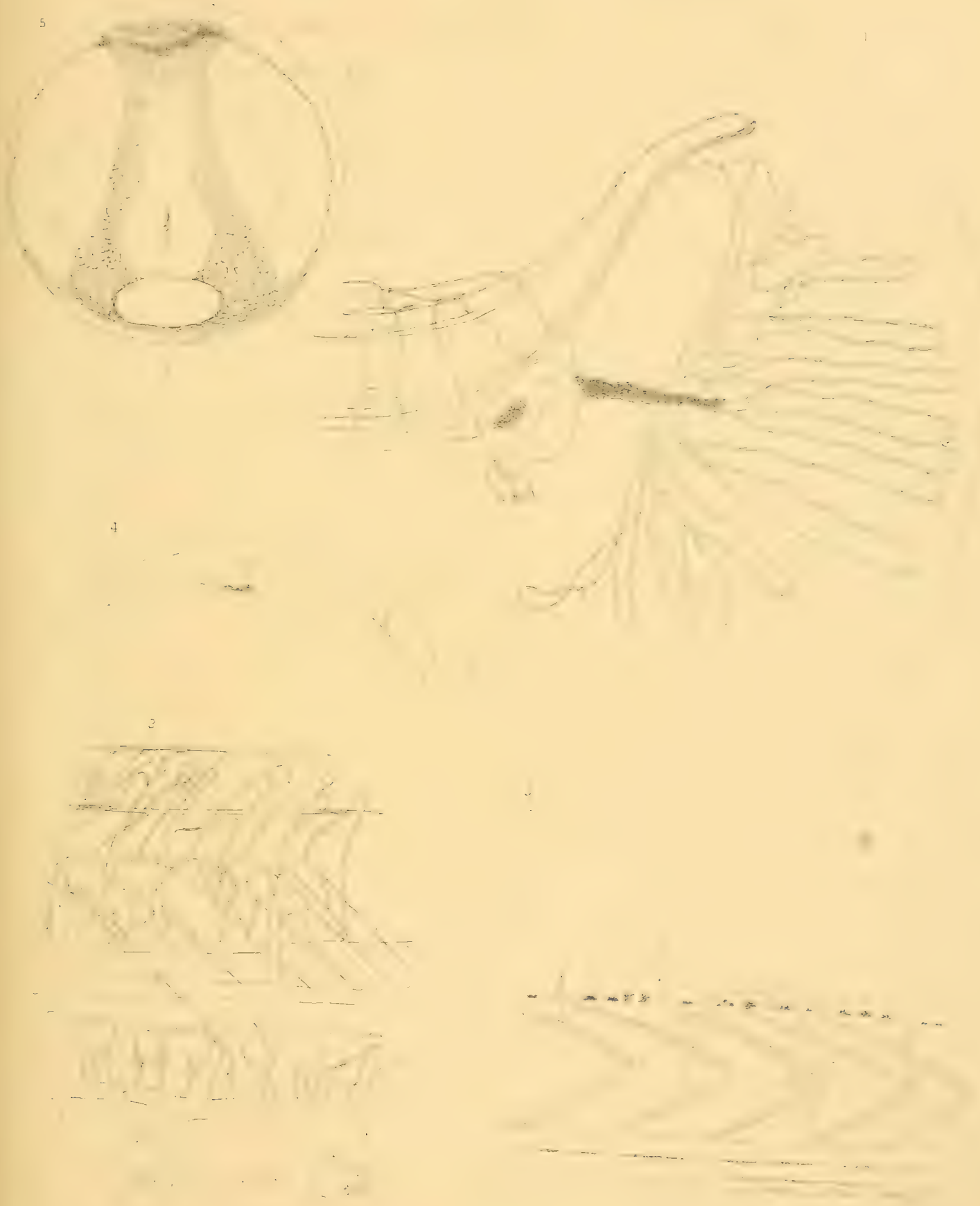
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